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VOL.
34
1953

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INNEHÅLL

P. A. J. Ryke: The ontogenetic Development of the somatic Musculature of the Trunk of the Aglossal Anuran Xenopus laevis 1

A. W. Crompton: The Development of the Chondrocranium of Spheniscus demersus with special Reference to the Columella auris of Birds 71

Nils Holmgren: On the "Horizontal Pit-line" in teleostomian Fishes 147

Harry Bergquist: On the Development of Diencephalic nuclei and certain mesencephalic Relations in *Lepidochelys olivacea* and other Reptiles 155

Giuseppe Colombo: L'oogenesi negli Ortotteri. I. Ricerche istologiche e citometriche in *Anacridium aegyptium* L. dalla schiusa all'imagine 191

Saad Hafez: Patterns of Mating Behaviour in the Domestic Buffalo 233

Ivo Poglayen-Neuwall: Untersuchungen der Kiefermuskulatur und deren Innervation bei Schildkröten 241

Ole Venge: The Sex Ratio in Farm Mink 303

VOL.
34
1953

THE ONTOGENETIC DEVELOPMENT OF THE SOMATIC MUSCULATURE OF THE TRUNK OF THE AGLOSSAL ANURAN XENOPUS LAEVIS (DAUDIN)

BY

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(With 30 text-figures.)

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CONTENTS

I. Introduction 2
II. Material and technique 4
III. Acknowledgements 5
IV. Own investigations 5
A. The pre-metamorphic stages 5
1. Early differentiation of the somites 6
2. The dorsal somatic musculature 8
3. The ventral somatic musculature 13
4. Zonal muscles covering the trunk 19
B. Metamorphosis 20
1. The dorsal somatic musculature 21
2. The ventral somatic musculature 26
3. Zonal muscles covering the trunk 30
C. The early post-metamorphic stage 30
1. Muscles of the vertebral column 30
2. Muscles of the abdominal wall 34
3. Zonal muscles covering the trunk 40
V. Discussion 42
1. Development of the somatic muscles in general 42
2. Developmental and adult conditions of specific muscles 47
a. General topography 47
b. Muscles originating from the m. dorsalis trunci 49
c. Muscles originating from the "Urwirbelfortsatz" 54
d. Zonal muscles of the trunk 58
3. Adaptations and affinities of *Xenopus* 59
VI. Short description of stages of *Xenopus* 62
VII. General résumé 64
VIII. References to literature 66
IX. Alphabetical list of abbreviations used in the figures 69

ABSTRACT

The secondary somatic muscles of the trunk develop by means of proliferations from the primary muscles. The dorsal part of the "Urwirbelfortsatz" contains the elements of both the m. obliquus abdominis internus and m. obliquus abd.

externus. The m. ileolumbalis of the adult is formed by the fusion of the m. ileolumbalis, pars medialis and pars lateralis. A separate m. coccygeo-sacralis is present in the young post-metamorphic stage. A true horizontal myoseptum is absent. A well-developed m. rectus abdominis superficialis can be distinguished during metamorphosis and even in the young post-metamorphic stage. The ontogenesis proves the allegedly primitive features concerning the m. rectus abdominis, the m. ileolumbalis and the m. coccygeo-sacralis to be specializations. *Xenopus* must be regarded as a very specialized anuran.

I. INTRODUCTION

A survey of the literature dealing with the muscular system in general and its development in particular reveals that the investigations hitherto conducted on this subject were, in many cases, rather inadequate, and have caused considerable confusion. In fact, except for a few fragmentary contributions, the 20th century produced nothing constructive to elucidate the structure, development and homologies of the muscles of the trunk. Owing to the non-existence of a recent, thoroughly reliable, publication on the ontogenesis of these muscles in *Urodela* and *Anura*, we still have to rely on the monographs of MAURER, investigations which ended in 1892 and 1895 respectively. ROMER (1942, p. 231) is of opinion that: "Lack of embryological investigation appears to have been due to the general belief that little of value could be obtained from the early history of such plastic material as limb muscle tissues." Probably this is a universal belief applicable among others to the ontogenesis of the whole muscular system.

I do not intend reviewing the literature prior to MAURER, as it has been fully dealt with by this author in his above-mentioned works. Suffice it to say, that these include the publications of MECKEL (1828), DUGÈS (1835), STANNIUS (1854), HUXLEY (1873), GOETTE (1875), SCHNEIDER (1879) and KÄSTNER (1892). The outstanding contribution towards the myology of the adult anuran undoubtedly is the account given in "Ecker's und Wiedersheim's Anatomie des Frosches", elaborated by GAUPP. Of the few anuran *Amphibia* whose muscular systems have been described in detail during the last fifty years the descriptions for *Xenopus* (GROBBELAAR, 1924) and *Bufo* (BIGALKE, 1926) are outstanding. On the whole, however, the ontogenesis has been neglected and even MAURER (1906) skims this problem in the well-known Hertwig's "Handbuch". The contribution of NISHI (1938) regarding the comparative anatomy of the anuran muscles in Bolk's "Handbuch" is unreliable and incomplete. There are, however, some notable contributions in connection with the limb musculature (FÜRBRINGER, ROMER, HOWELL) and the muscles of the head (LUTHER, LUBOSCH, EDGEWORTH). The greatest authority on comparative myology during the 20th

century undoubtedly was VERSLUŸS of Vienna, as confirmed by his excellent contribution in the "Leerboek der vergelijkende ontleedkunde van de Vertebraten" (1924).

For our present knowledge concerning the early embryology of the musculature we are largely indebted to the classical embryologists GOETTE and RABL. Their works, although containing many errors, furnished the foundation for subsequent research of the differentiation of the mesoderm. The literature on this subject reveals great confusion as to the terminology of the primary units from which the axial skeleton, axial connective tissue and the somatic musculature develop. Terms such as primitive segment, protovertebra (= Urwirbel), somite, sclero-myotome, myotome and myomere are often used vicariously. GADOW and ABBOTT (1895) subjected the use of these terms to a critical analysis, and for further details the reader is referred to their work. In order to avoid the possibility of misinterpretation and confusion, the definitions given below will be adhered to in this paper.

OL.
34
953

The somites ("Urwirbel", RABL, 1889, 1893) are the segmentally arranged dorsal coelomic pouches. The cavity of the somite is the "Urwirbelhöhle" or myocoel bounded by a continuous medial and lateral lamella. The latter is known as the dermatome, since its epithelium is chiefly differentiated into the connective tissue cells of the cutis. The dorsal and medial portions of the medial lamella are known as the myotome, since its epithelium is differentiated into the somatic muscles. The ventro-medial portion of this lamella proliferates the cell mass known as the sclerotome.

The initial indications of metamerism in the vertebrate body are retained only in the sclero-myotome and dermatome. After separation of the dermatome (to form the cutis) the somite consists of the sclero-myotome. At this stage the somite is potentially blastogenic (axial connective tissue and future axial skeleton) and myogenic (somatic muscles). That part which gives rise to the axial mesenchyme is termed the sclerotome and is situated on the ventro-medial side of the somite. The remaining portion of the sclero-myotome is the myotome itself giving rise to somatic muscle fibres. In *Amphioxus* the sclerotome develops a central cavity, the sclerocoel (bounded laterally by a skeletogenous and medially by a fasciogenic lamella), but in *Amphibia*, as in the majority of fishes, it hardly ever develops in this fashion. In these groups the sclerotome appears as a cell proliferation on the medio-ventral side of the somite. RABL in his "Theorie des Mesoderms" (1889, 1893) was the first to realize the homology between these axial mesenchyme cells and the sclerotome of *Amphioxus*. His theory was fully accepted by later workers like FRANZ (1925), who proved that both sclerotome and axial mesenchyme arise from the somite at the level of the dorsal aorta, and by the discovery in some fishes of a sclerotome with a sclerocoel by D'ANCONA (1925).

The numbers used in the text to indicate the ontogenetic stages of *Xenopus*

correspond to those of the Normal Table which is being prepared by the Hubrecht Institute in Utrecht, Holland. These stages are briefly described at the end of the discussion. The muscle terminology used in this dissertation is mainly that of GAUPP (1896), and any deviations from his system are indicated. Concerning other terminologies the reader is referred to HOFFMANN (1873—1878), GAUPP (1896) and BIGALKE (1926).

As may be expected, the pre-metamorphic ontogenesis of the muscles of the trunk proceeds in essentially the same manner as those of other *Amphibia* described by previous authors. This picture, however, changes considerably during and after metamorphosis, as is the case in the vast majority of *Anura*. Apart from certain anatomical peculiarities, the persistence of the lateral line sense organs in the adult stage, indicates that extraordinary anatomical relations can be expected. This neotenic feature also directs attention to the danger of drawing phylogenetic or other conclusions based merely on ontogenetic data; these nevertheless, remain the main criterion in determining the relationships.

The major problems arising from the study of the ontogenesis of the muscles of the trunk are:

1. Connotation of the term mesenchyme.
2. The development of the primary muscles.
3. The interpretation of the elements present in the "Urwirbelfortsatz".
4. The ontogenetic origin of the secondary muscles.
5. The similarity between the muscles of the early post-metamorphic *Xenopus* and those of other more adult *Anura*.
6. The interpretation of neotenic and "primitive" characteristics of *Xenopus*.
7. The "adaptations" of *Xenopus* to an aquatic habitat.

II. MATERIAL AND TECHNIQUE

The specimens of *Xenopus* used for this investigation were collected in Jonkerhoek, near Stellenbosch, by Mr. J. Faber of the Hubrecht Laboratories, Utrecht, Holland. They will also be used for the preparation of certain parts of the Normal Table, of *Xenopus*, the data of which are being collected by the above-mentioned Institute. For the present paper approximately 100 specimens were used. These covered stages 20 to 66, classified according to the instructions of the Hubrecht Laboratories.

The material was fixed in "Lenhossek-fluid", consisting of a mixture of saturated mercuric chloride (75 parts), alcohol 50 % (25 parts), and glacial acetic acid (5 parts) saturated with picric acid. Stages 20—48 were preserved in n.-isobutyl-alcohol and the rest in 80 % ethyl-alcohol. The older specimens were decalcified in nitric acid alcohol and cleared in methyl-benzoate-celloidin.

With few exceptions all the specimens were sectioned both transversely and

sagittaly, and frontal sections of the earlier stages proved to be most valuable. The thickness of the sections varied from 8 μ in the young up to 15 μ in the older stages.

Bulk staining with borax carmine and counterstaining with azan was less satisfactory for some stages. The bleu de Lyon and Bismarck brown method was successfully adopted for other specimens. This staining method was employed by using a relatively weak 70 % alcoholic solution of bleu de Lyon and a concentrated aqueous solution of Bismarck brown.

For the purpose of obtaining a base-line to serve as a guide for making reconstructions, rectangular liver slabs were embedded underneath each specimen. A slight modification of the base-line technique employed by VAN EEDEN (1951) proved to be satisfactory.

Several large adult specimens of *Xenopus,* also obtained from Jonkershoek, were dissected and examined macroscopically. For purposes of comparison I had access to the prepared material of *Ascaphus truei,* kindly placed at my disposal by my colleague, Dr. J. A. VAN EEDEN.

VOL. 34 1953

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I wish to record my gratitude to Prof. C. A. DU TOIT under whose supervision this investigation was carried out. My sincere thanks are due to Prof. C. G. S. DE VILLIERS for constructive criticism and encouragement.

I am deeply indebted to Dr. J. A. VAN EEDEN for many helpful suggestions and for placing the series of *Ascaphus* at my disposal; to Prof. G. T. S. EISELEN for the facilities which I have enjoyed in the Zoological Institute of the Potchefstroom University for C. H. E.; and to the Council for Scientific and Industrial Research for the financial assistance which made this investigation possible.

My thanks are also due to the Hubrecht Laboratories, Utrecht, Holland, for placing the material of *Xenopus* at my disposal. I am especially appreciative of the technical aid given by my wife in preparing the typescript.

IV. OWN INVESTIGATIONS

A. THE PRE-METAMORPHIC STAGES

It is generally accepted that the primary somatic musculature of vertebrates originates from myoblast cells derived from the myotomes. It is, however, a well-known fact that these myoblast cells are not the sole contributors to the development of somatic muscles. SCHMIDT (1925) and KATZNELSON (1934 a, b)

are the chief exponents of the theory that "part of the striated musculature of vertebrates is derived by means of local differentiation from the mesenchyma." There is, however, considerable difference of opinion as to the origin of this "mesenchyma" participating in the formation of secondary muscles. Myoblast cells and *axial* mesenchyme are both derivatives of the somites, more specifically, the sclero-myotome, which gives rise to the axial skeleton and the somatic striated skeletal muscles. Exceptions to this general statement are the muscles of the heart and visceral arches which, although derived from lateral mesoderm, are striated.

The present investigation covers only that part of the somatic musculature developing between the head and the tail. Although it is impossible to determine exactly what part of the body represents the trunk in the early larval stages, it was found possible, by making use of the fact that the musculature is segmented into myomeres, to determine this region by commencing with the examination of the more adult stages and proceeding towards the younger larvae. The anlagen of the somites from which the myomeres are derived, can be observed externally at the end of neurulation (Stage 19). The relation of myotomes to other developing organs can best be observed in transverse sections, but horizontal sections naturally show more clearly, the number of myotomes with their longitudinal metameric arrangement laterally to the central nervous system and the notochord.

VOL
34
195

1. *Early differentiation of the somites*

The anlagen of the somites are followed by a rapid differentiation into the different portions mentioned previously. For a full and accurate account the reader is referred to the excellent works of MAURER on the development of the muscles of the trunk of *Urodela* (1892) and *Anura* (1895). Although these investigations were carried out approximately sixty years ago, the results obtained are still regarded as standard for the *Amphibia*. Maurer's views on the process of the differentiation of the somites essentially agree with my own findings based on the ontogeny of *Xenopus laevis*.

According to Mr. Faber, the first indication of any reaction to an external stimulus may be observed during the stages at which the eye-, jaw- and gill-primordia are formed (Stages 22—24). These also, are the stages in which the transformation of the epithelial-like myoblast cells into spindle-shaped cells forming the myofibrils, takes place. In collaboration with my co-worker, Mr. Smit, we were able to determine the presence of one somite infront of, and three pre-trunk somites behind the ear vesicle (Stage 24). For a description and illustrations of these somites anterior to the trunk the reader is referred to the work of SMIT (in press). The present investigation concerns only the trunk myotomes, i.e. from the 4th one behind the ear vesicle backwards.

At the stage following the anlage of the ear vesicle (23) the somites are

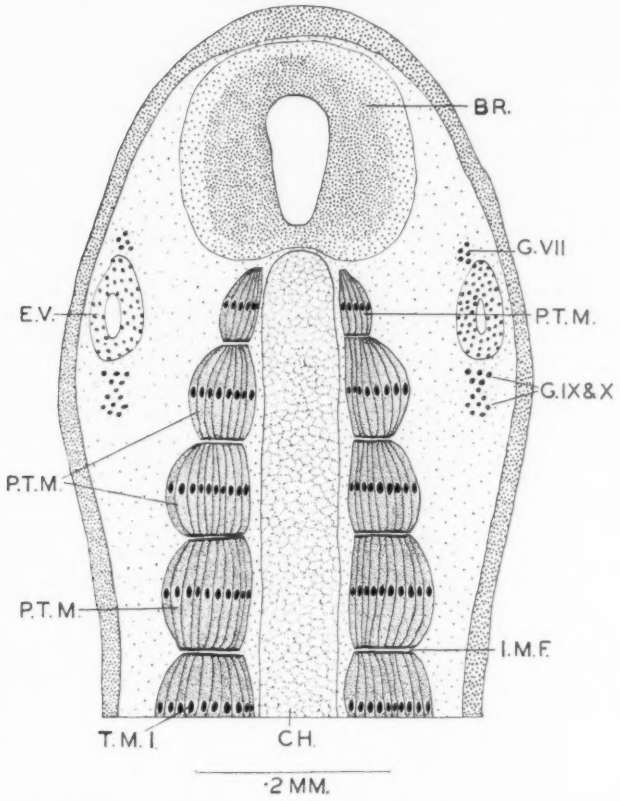

Fig. 1. Frontal section through the anterior myotomes. Stage 24. *BR.* brain; *G.* ganglion; *P.T.M.* pretrunk myotome; *I.M.F.* intermyotomic fissure; *T.M.* trunk myotome; *E.V.* ear vesicle.

situated on either side of the central nervous system and notochord, while the ectoderm serves as an external covering. The hypochorda and aorta have not yet developed. Three distinct divisions can be distinguished in each somite: a lateral lamella (dermatome) consisting of cuboidal epithelial cells; dorsally this layer is confluent with the medial or muscle lamella consisting of more than one layer and constituting the myogenic portion of the sclero-myotome; the third division can be seen as a projection on the medio-ventral side of the myotome and represents the sclerotome. It is also evident that, as maintained by MAURER for other *Amphibia*, the ventral surface of this projection is continuous with the splanchnopleura of the alimentary tract in the same manner as the cutis layer (dermatome) is inseparable from the dorsal part of the somatopleura. The caudally situated trunk somites, however, show no indications of developing sclerotomic projections. The myotome cells of this region are still typical myoblast

cells, whereas those of the anterior somites are partly composed of clearly visible spindle-shaped myofibrils (fig. 1). In frontal sections it can be seen that each of these fibrils has a large oval nucleus. The fibrils are longitudinally arranged, and the bundles into which they are grouped match the fusiform shape of the individual fibrils. In surface view approximately ten fibrils are visible in each bundle. These metamerically arranged spindle-shaped bundles are not connected with one another but are separated by means of intermyotomic fissures. During later ontogeny these fissures between consecutive myotomes are filled up with cells migrating from the axial mesenchyme.

In the subsequent stages new somites are added and the existing ones are further differentiated. The anteriorly situated somites develop more rapidly, with the result that the posterior ones of older stages correspond, in degree of development, to the anterior ones of previous stages.

Distinctive of stage 30 is the separating off of the sclerotome cells from the sclero-myotome, the remaining portion being the myotome proper. The cutis cells become apposed to the medial surface of the ectoderm.

Subsequently a mass of cells ("Urwirbelfortsatz" of Maurer) projecting ventrally from the ventro-lateral side of the myotome, can be observed (fig. 27). This projection indicates the beginning of the formation of the ventral somatic muscles of the trunk. In subsequent stages it spreads more ventrad between the cutis and the somatopleura. Contrary to the condition in *Urodela* (MAURER, 1892) the "Urwirbelfortsatz" becomes detached from the dorsal somatic musculature. In *Xenopus* this is accomplished at approximately stage 38. As in most other developmental processes this migration of the myotome cells proceeds in a rostro-caudal direction, the more posteriorly situated projections being formed during stages later than the anterior ones. Even in stage 40 the hindmost "Urwirbelfortsätze" are still connected with the dorsal somatic musculature. It is, however, obvious that these ventrally migrating somatic muscles are confined to the region of the trunk. In the subsequent stages the existing conditions are elaborated. The dorsal and ventral musculature of the trunk become completely separate, and each of these masses of muscles develops independently to provide for the locomotory needs of the larval and the adult form.

2. *The dorsal somatic musculature*

At the stage in which the mouth breaks through (Stage 40) two pre-trunk myotomes are present. The vagus-group ganglion lies antero-laterally to trunk myotome I. A nerve tract stretches obliquely forwards between the central nervous system and the jugular ganglionic mass. It is presumably associated with trunk segment I.

The next three stages show little alteration in the general plan of the dorsal musculature, except for the disappearance of the penultimate pre-trunk myotome

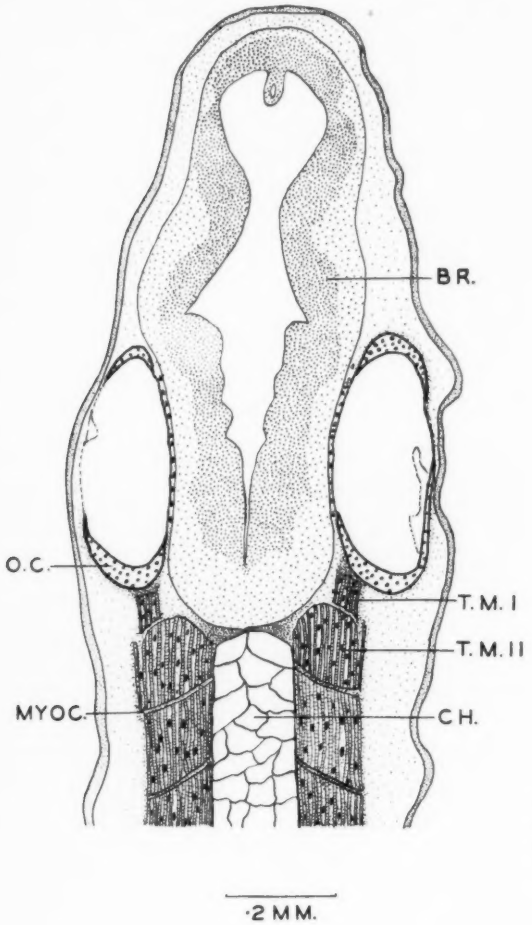

Fig. 2. Frontal section through the anterior myotomes and notochord. Stage 47. *Br.* brain; *T.M.* trunk myotome; *CH.* chorda dorsalis; *O.C.* otic capsule; *MYOC.* myocomma.

(Stage 45). During these stages axial mesenchyme steadily migrates into the intermyotomic fissures between consecutive myotomes. The cells constitute connective tissue layers, the transverse myosepta (auctorum) or myocommata, to which the anterior and posterior ends of the fibres of two consecutive myotomes are attached. The designation myocomma is preferable to that of myoseptum transversum because of possible confusion with the horizontal myoseptum (see Discussion). The myocommata, therefore, are situated intermetamerically in contrast to the metameric arrangement of the myotomes.

Stage 46, with one pre-trunk myotome still present, shows the jugular ganglion lying laterally to the myocomma between trunk myotomes I and II. During the next stage this remaining pre-trunk myotome disappears and trunk myotome I is reduced to a few fibres joining trunk myotome II to the posterior wall of

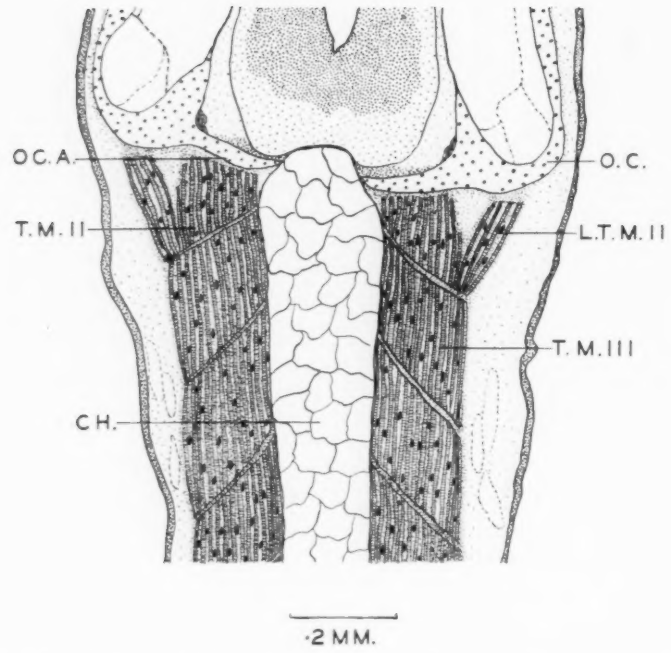

Fig. 3. Frontal section through the anterior myotomes. Stage 48. *O.C.* otic capsule; *L.T.M.* lateral portion of trunk myotome; *T.M.* trunk myotome; *CH.* chorda; *OC.A.* occipital arch.

the otic capsule (fig. 2). The latter myotome is divisible into a ventral portion lying laterally to the notochord, and a dorsal part covering the lateral and dorso-lateral surfaces of the central nervous system. The anterior half of this myotome is completely separated into dorsal and ventral portions. The posteriorly situated myotomes are similar to the posterior half of myotome II. Some of the fibres of the latter are being separated off from the main part of the myotome, and in the next stage (Stage 48) extend laterally to form a complete independent portion (fig. 3), which inserts itself onto the cartilaginous postero-lateral wall of the otic capsule. The medio-ventral fibres of this myotome are inserted onto the posterior surface of the developing occipital arch, whereas their posterior ends are attached to the myocommatal aponeuroses between the IInd and IIIrd trunk myotomes. The myocommata between all the myotomes are distinct, and the nuclei of the connective tissue cells are clearly indicated.

Apart from the firmer attachments of the muscles, due to the development of the skeletal structures, the subsequent stage (49/50) is much the same as the previous one. The dorsal portion of trunk myotome II covers the dorsal surface of the occipital arch and the postero-dorsal surface of the auditory capsule. The lateral bundle still inserts itself onto the postero-lateral surface of the auditory capsule, but does not exhibit as much individuality as in the

VOL.
34
1953

previous stage. The medial fibres of this myotome are inserted onto the lateral and ventral surfaces of the occipital arch. In the next stage these fibres are much reduced in number. Very soon afterwards they are obliterated by the developing atlas and the second vertebra (Stage 52). It is possible that at least some of the most medial of these fibres joined those of trunk myotome III. The latter lies laterally to the notochord, and its anterior border is immediately behind the cartilage formed by the fusion of the occipital arch with the anlagen of the atlas and the second vertebra. During the next stages, however, the first two vertebrae rapidly become extended, resulting in displacement of their position relative to this myotome. The latter now covers approximately the entire lateral surfaces of these two vertebrae. The fibres of the IVth myotome of the trunk run along the lateral surface of the third vertebra. The rest of the myotomes exhibit similar relations to their corresponding vertebrae (Stage 52).

During the preceding two stages (51, 52) the anlagen of the "short" muscles of the vertebral column can be observed (fig. 4). They develop between consecutive vertebral arches and are known as the mm. interarcuales. There is no doubt that they develop as derivatives of the dorsal musculature (= m. dorsalis trunci) by means of cell proliferations from their dorsomedial aspects. Such proliferations migrate ventrad in the connective tissue and are probably transformed into new muscle fibres. Although the participation of mesenchymatous cells (histologically) in their construction cannot be demonstrated the possibility cannot be excluded. During the early stages of development of the mm. interarcuales 10 consecutive pairs can be distinguished. The first pair stretches between the occipital arch and the atlas, the last pair between the 9th and 10th vertebrae (fig. 5). The latter vertebra participates in the formation of the urostyle during metamorphosis. It is of major importance to realize that these muscles are not merely separated fibres of the m. dorsalis trunci but are secondary muscles which develop by means of transformation of muscle cells originating from the myotome. There are, however, during the last stages of the pre-metamorphic period, a secondary tendency towards closer association with the m. dorsalis trunci.

The last few stages prior to metamorphosis show little change in the composition of the dorsal musculature. Trunk myotome II is represented by a dorsomedial muscle plate gradually extending in an anterior direction. In the last stage before the actual metamorphosis (Stage 57) it approximately covers the whole dorsal and dorso-lateral roof of the otic and occipital region. The dorsal roof of the brain case is devoid of any muscles. In the medio-dorsal line the myotomes are inserted into a thick connective tissue strip, the fascia intermuscularis (figs. 4 and 5).

The medial portion of trunk myotome III inserts onto the ventro-lateral surface of the atlas and the lateral surface of the second vertebra. Likewise each of the posteriorly situated myotomes is attached to the corresponding sur-

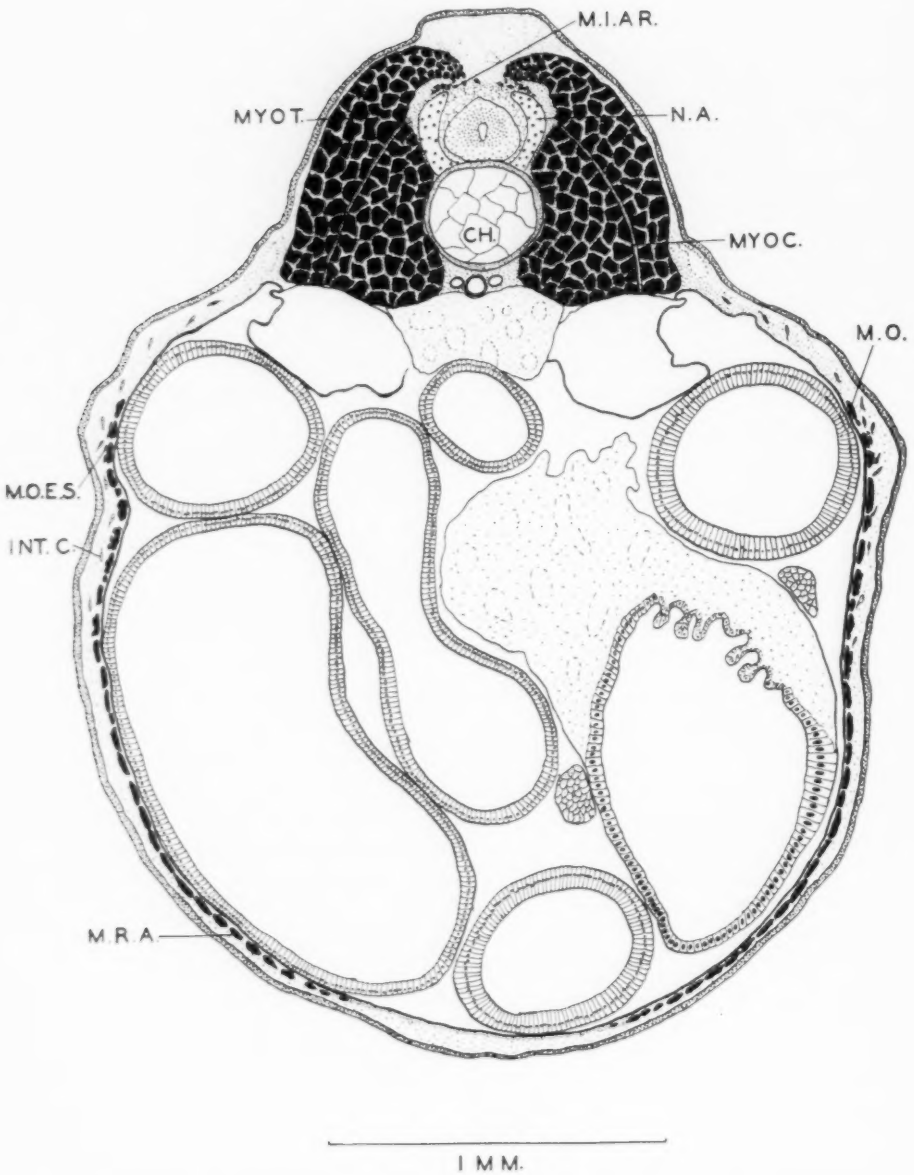

Fig. 4. Transverse section through the trunk to show the anlagen of the mm. interarcuales and m. obliquus abdominis externus superficialis. Stage 51. *M.I.AR.* m. interarcualis; *N.A.* neural arch; *MYOC.* myocomma; *M.O.* m. obliquus abdominis; *M.R.A.* m. rectus abdominis; *INT.C.* intermediate cells; *M.O.E.S.* m. obliquus abdominis externus superficialis; *MYOT.* myotome (m. dorsalis trunci).

VOL. 34 1953

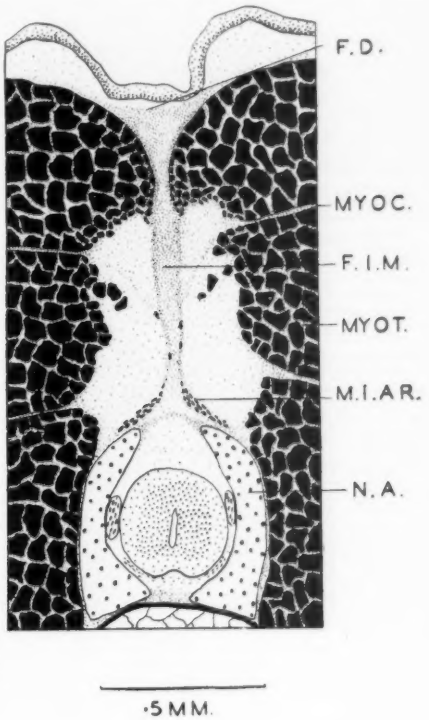

Fig. 5. Transverse section through the dorsomedial part of the trunk. Stage 51. *F.D.* fascia dorsalis; *MYOC.* myocomma; *F.I.M.* fascia intermuscularis; *MYOT.* myotome (m. dorsalis trunci); *M.I.AR.* m. interarcualis; *N.A.* neural arch.

faces of two vertebrae. During this stage (57) the three pairs of ribs, corresponding to the 2nd and 3rd and 4th vertebrae, are developing in the myocommata between myotomes III and IV, IV and V and V and VI respectively.

There are also indications of the development of another set of "short" muscles in connection with the vertebral column. These are the mm. intertransversarii, formed by means of the transformation of muscle cells on the medial side of the myotome (m. dorsalis trunci). As the name indicates, they stretch between consecutive transverse processes during later stages.

3. *The ventral somatic musculature*

The manner of development and the identification of the separate muscles in the ventrally migrating musculature led to controversies amongst the earliest workers in this field. For the elucidation of facts concerning this problem we once more are indebted to MAURER (1892, 1895). It has already been mentioned that the "Urwirbelforsatz" becomes detached from the dorsal longitudinal muscles of the body. My investigations on *Xenopus*, corroborate MAURER'S findings concerning the primitive anlage of the first ventral muscle of the

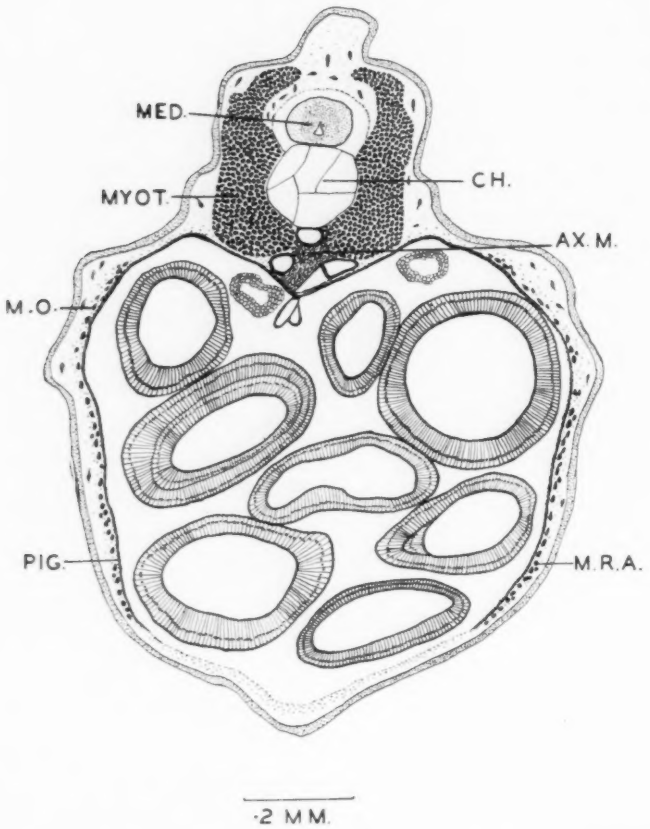

Fig. 6. Transverse section through the trunk to show the primary musculature. Stage 46. *MED.* medulla spinalis; *MYOT.* myotome (m. dorsalis trunci); *M.O.* m. obliquus abd.; *PIG.* pigment layer; *M.R.A.* m. rectus abdominis; *A.X.M.* axial mesenchyme; *CH.* chorda dorsalis.

trunk. Initially it appears as a double row of cells, the lateral lamella of which gradually disintegrates and disappears. At the time, when the cells of the medial lamella are transformed into muscle fibres, the ventral musculature practically consists of one single muscle. For a relatively long period this muscle is the only muscular covering of the abdominal cavity (fig. 6).

An anterior bundle of this muscle—the bulk of which consists of 5—6 fibres—inserts onto the medio-ventral surface of the hyoid and the lateral wall of the pericardial sac. Its most anterior insertion is in the same vertical plane as the anterior border of trunk myotome I. A slender ventral portion of this anterior bundle inserts into the medial wall of the last gill pouch. Posteriorly to the heart the ventral musculature becomes a thin plate, 1—2 fibres thick, covering the ventro-lateral part of the body cavity. Caudally behind

VOL. 34 1953

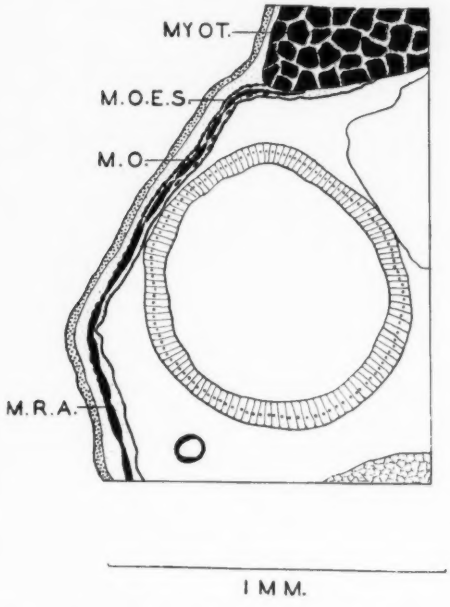

Fig. 7. Transverse section through the lateral portion of the trunk to show the delamination of the m. obliquus abd. externus superficialis. Stage 52. *MYOT.* myotome (m. dorsalis trunci); *M.O.E.S.* m. obliquus abd. externus superficialis; *M.O.* m. obliquus abdominis; *M.R.A.* m. rectus abdominis.

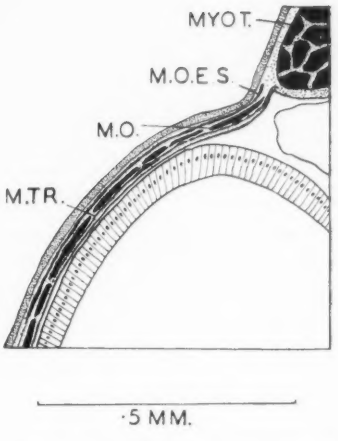

Fig. 8. Transverse section through the anlage of the m. transversus abdominis. Stage 53. *MYOT.* myotome (m. dorsalis trunci); *M.O.E.S.* m. obliquus abd. externus superficialis; *M.O.* m. obliquus abdominis; *M.TR.* m. transversus abdominis.

the pronephros, this plate reaches to approximately the ventro-lateral border of the dorsal myomeres and simulates the conditions in the anterior part of the trunk during previous stages.

Judging from my own observations and comparing them with those of MAURER, it is evident that the ventral part of this muscle must represent the musculus rectus abdominis of the adult, whereas the dorsal part contains the elements of the m. obliquus abdominis externus and m. o abd. internus. Compared with the slight oblique inclination of the fibres of the m. obliquus abd. those of the m. rectus abd. run in a strictly longitudinal direction. It must, however, be stressed that there is no distinct line of demarcation between m. obliquus abd. and m. rectus abd. — except perhaps for the more compact nature of the muscle bundles of the latter (fig. 6). I cannot at this stage neglect to draw attention to the presence of several mesenchyme-like, probably amoeboid, cells on the lateral and medial surfaces of the m. obliquus abd. Whether these cells are pre-muscular or intermediate cells assisting in the transformation of the muscle cells, cannot be determined with certainty.

There is very little change in the general composition of the ventral musculature up to the stage when the fore-limbs become visible (Stage 50). The muscle inserts itself onto the posterior surface of the ventral part of the hyoid, whereas the slender ventral portion still attaches itself to the medial wall of the gill pouch and the pericardium. In the medio-ventral line the m. rectus abd. lies against the linea alba, a connective tissue band derived from migrant axial mesenchyme. Stage 51 exhibits a denser concentration of the above-mentioned mesenchyme-like cells on the inner and outer surfaces of the m. obliquus abd. They are entirely absent from the area of the m. rectus abd. At the same time the development of the secondary muscles is indicated by superficial proliferations on the lateral side of the m. obliquus abd. (figs. 4 and 7). This constitutes the beginning of the formation of the m. obliquus abd. externus superficialis. The subsequent stage (52) exhibits similar conditions on the medial side of the m. obliquus, resulting in the anlage of the m. transversus abd. (fig. 8). The dorsal myotomes take no part in the construction of these two secondary muscles, the m. obliquus abd. being the chief source from which they arise.

VOL.
34
1953

The rôle of the amoeboid mesenchyme-like cells cannot be determined, and their significance is probably physiological rather than morphological.

In comparing the development of the m. obliquus abd. externus superficialis with the m. transversus abd., the striking feature probably is the rapid extension of the former during subsequent stages (see Discussion). As in the case of the dorsal secondary muscles, these two new coverings of the abdominal wall are constructed by means of liberated cells which are rebuilt and transformed into muscle fibres. They are constantly being thickened by the addition of elements arising from the remaining parts of the m. obliquus abd. After the complete separation of these secondary muscles from the m. obliquus abd., the latter represents a fused m. obliquus abd. externus profundus and m. obliquus abd. internus. MAURER considered the dorsal part of the "Urwirbelfortsatz" as representing only the m. obliquus abd. internus and that the development of the m. o. e. superficialis represents the first appearance of the entire m. obliquus abd. externus. My own investigations do not, however, support this view (see Discussion).

The extent of the remaining m. obliquus abd. can be determined after the formation of the secondary muscles. Its demarcation from the m. rectus abd. is indicated by the connective tissue to which the m. transversus abd. is attached (fig. 9). At this stage the dorso-lateral surfaces of the original m. obliquus abd. are covered medially by the m. transversus abd. and laterally by the m. obliquus abd. externus superficialis. The m. rectus abd. is strongly developed and is more compact than the m. obliquus abd.

In the next two stages (55—56) the existing conditions are continued and consolidated. The m. obliquus abd. externus superficialis is more prominent

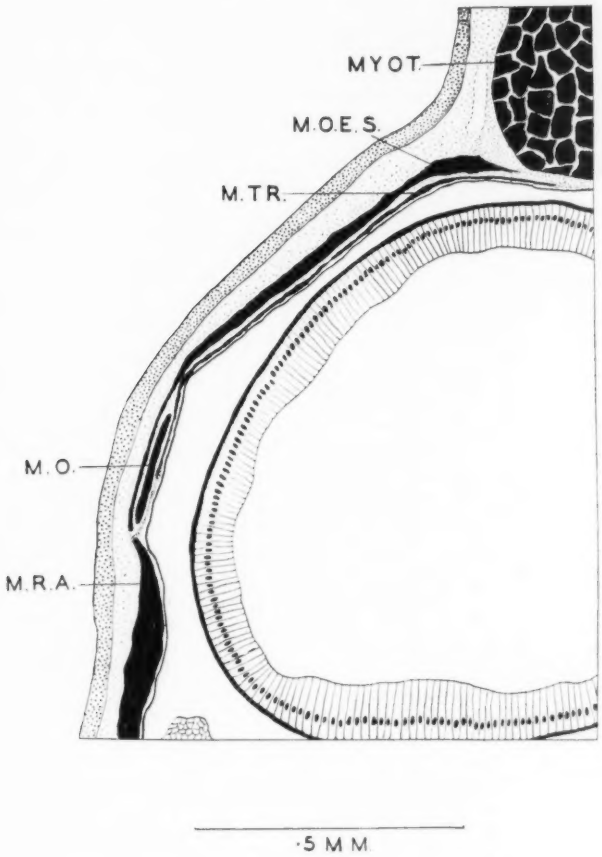

Fig. 9. Transverse section through the lateral part of the trunk to show the demarcation between the m. rectus abdominis and m. obliquus abd. Stage 55. *MYOT.* myotome (m. dorsalis trunci); *M.O.E.S.* m. obliquus abd. externus superficialis; *M.TR.* m. transversus abd.; *M.O.* m. obliquus abd.; *M.R.A.* m. rectus abdominis.

and much better developed than the m. transversus abd., the direction of fibres of which cannot, as yet, be determined. The m. transversus abd. covers the dorso-lateral aspect of the abdominal cavity, whereas the superficial external oblique muscle stretches backwards to approximately the level of trunk myotome VIII. The m. rectus abd. reaches caudad to the level of trunk myotome IX.

Topography, origins and insertions of the ventral somatic muscles of the trunk in the last stage before the actual metamorphosis, are as follows:

The massive anterior bundle of the m. rectus abd. inserts itself onto the postero-ventral surface of the hyoid, its fibres running in a sligthly postero-ventral direction. The medial fibres are attached to the lateral wall of the

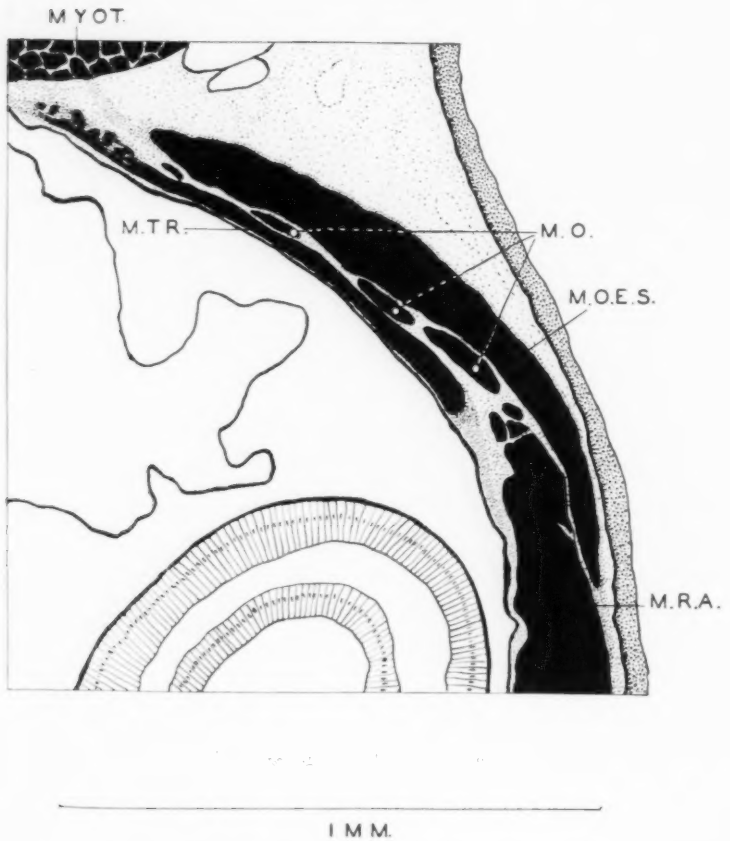

Fig. 10. Transverse section through the remaining fibres of the m. obliquus abdominis. Stage 57. *MYOT.* myotome (m. dorsalis trunci); *M.TR.* m. transversus abd.; *M.O.* m. obliquus abd.; *M.O.E.S.* m. obliquus abd. externus superficialis; *M.R.A.* m. rectus abdominis.

pericardium and the slender ventral portion, consisting of superficial fibres, still exists as such. Posterior to the heart the whole muscle broadens and flattens out where it meets fibres of the m. obliquus abd. The ventro-medial fibres do not approach the middle line very closely. Behind the shoulder girdle the m. obliquus abd. externus superficialis and m. transversus abd. are well-developed. They attach themselves to the myocomma between trunk myotomes IV and V. The m. o. abd. e. superficialis is a thick muscle plate covering both the primary m. obliquus abd. and the dorsal part of the m. rectus abd. The m. transversus is much thinner and is situated on the medial side of the m. o. abd. e. superficialis and the remaining parts of the primary m. obliquus abd. There are indications of segmentation in the m. obliquus abd. externus superficialis. The dorso-medial portion of the m. transversus abd., lying underneath the ventral

VOL. 34 1953

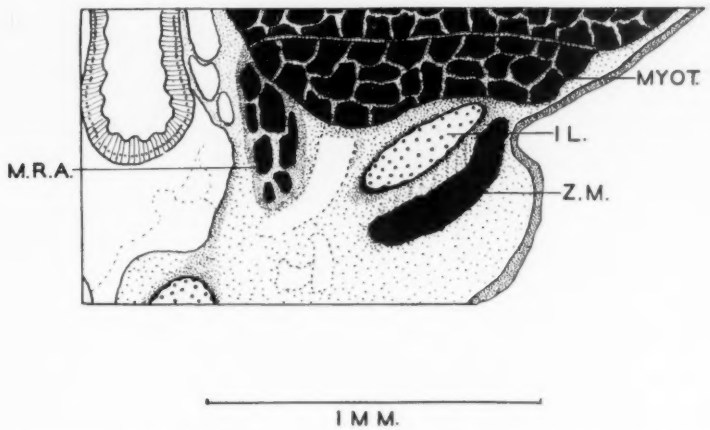

Fig. 11. Transverse section through the hinder part of the trunk to show the posterior continuation of the m. rectus abdominis. Stage 57. *MYOT.* myotome (m. dorsalis trunci); *IL.* ilium; *Z.M.* zonal muscle; *M.R.A.* m. rectus abdominis.

surface of the dorsal myomeres is composed of fibres, some of which run in a longitudinal direction and others running obliquely. Posteriorly the m. transversus stretches backwards as far as the hindmost border of dorsal myotome VII, whereas the m. obliquus abd. externus sup. reaches to the posterior border of myotome VIII. That part of the primary m. obliquus abd., left between the m. transversus and the superficial oblique muscle is not a compact muscle plate, but consists of independent bundles (fig. 10). The m. rectus abd. extends backwards to the hindmost border of myotome IX. An interesting point in the development of the m. rectus abd. is the occurence of a backwardly directed strip reaching to the root of the tail (fig. 11). It runs along the outer side of the cloaca and possibly represents the m. rectus lateralis of some fishes. During metamorphosis this muscle strip atrophies.

There are also indications of the anlage of a superficial muscle on the lateral surface of the m. rectus abdominis (fig. 12).

4. *Zonal muscles covering the trunk*

It is well-known, that in most *Tetrapoda* some of the muscles of the limbs or girdles can participate in covering the trunk. Likewise muscles of the trunk can serve as limb or girdle muscles e.g. the m. psoas of mammals. The zonal muscles of the trunk of *Xenopus*, as revealed by the present investigation, are the m. latissimus dorsi and the m. pectoralis, pars abdominalis associated with the shoulder girdle, and the m. iliacus externus taking origin from the pelvic girdle.

During the last few stages prior to the actual metamorphosis, the anlagen of

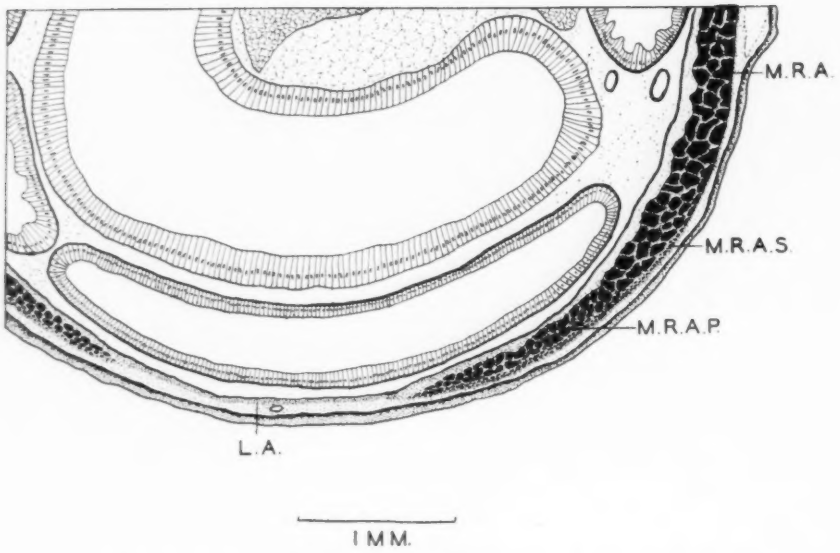

Fig. 12. Transverse section through the ventral part of the trunk to show the indications of the development of the m. rectus abdominis superficialis. Stage 57. *M.R.A.* m. rectus abdominis; *M.R.A.S.* m. rectus abdominis superficialis; *M.R.A.P.* m. rectus abdominis profundus; *L.A.* linea alba.

the m. latissimus dorsi and of the m. pectoralis, pars abdominalis can be observed respectively dorsal and ventral to the developing shoulder girdle. In a paper on the development of the shoulder girdle of *Xenopus* VAN PLETZEN (in press) mentions that there are indications that these muscles are of myotomic origin. According to my own observations there can be very little doubt that this actually is the case. Practically from the whole latero-ventral portions of the corresponding myotomes cells are proliferated and migrate in the direction of the limb bud (fig. 13).

During the last stage prior to metamorphosis the m. latissimus dorsi and the m. pect. p. abdominalis are not yet well developed and only cover that part of the musculature of the trunk in the vicinity of the shoulder girdle. The m. iliacus externus develops between the anterior part of the ilial wing and the muscles of the thigh. Topographically it serves as a lateral covering for part of the postero-lateral musculature of the trunk.

B. METAMORPHOSIS

The metamorphosis of the *Anura* is a stage of transition from an aquatic to a terrestrial mode of life, and this process must obviously be reflected in the development of the musculature. During the pre-metamorphic stages two sets of muscles are developed, the primary and the secondary group, the latter

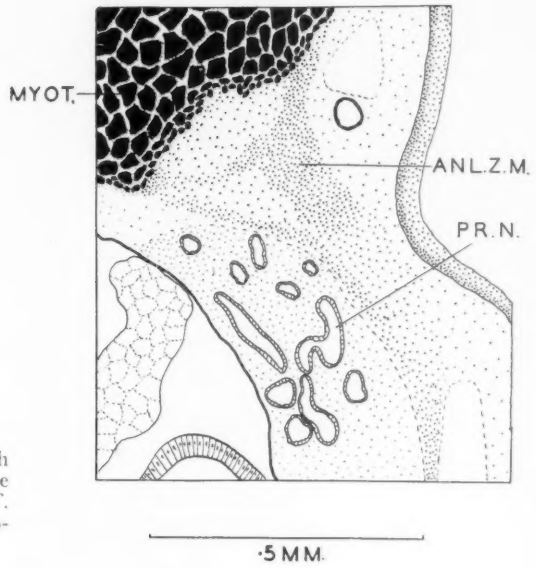

Fig. 13. Transverse section through the anlage of the muscles of the shoulder girdle. Stage 55. *MYOT.* myotome; *ANL.Z.M.* anlage of zonal muscles; *PR.N.* pronephros.

OL.
34
953

of which developed during the stages immediately preceding metamorphosis (see Discussion). During metamorphosis it is determined which of these sets of muscles will predominate in the adult form.

1. *The dorsal somatic musculature*

As can be expected, no sharp line of demarcation can be drawn between premetamorphosis and metamorphosis. The differentiation of the dorsal myotomes, which started before metamorphosis, resulted in the appearance of secondary muscles. The remaining part of the primary muscles, which still forms the bulk of the dorsal musculature, is known as the m. dorsalis trunci (fig. 6), whereas the secondary group is represented by the mm. interarcuales (= interspinales, intercrurales) (fig. 4) and by the mm. intertransversarii (fig. 14).

The m. dorsalis trunci, divided into myomeres by the myocommata, extends rostrad over the dorso-lateral surface of the otic and occipital regions, its foremost fibres being in close association with those of the m. interarcualis I. The second m. interarcualis, between the neural arches of the atlas and 2nd vertebra, have no connection with the m. dorsalis trunci, whereas the third and more caudally situated consecutive mm. interarcuales associate themselves with the dorso-medial fibres thereof. The lateral surface of the m. dorsalis trunci is partly covered by the suprascapula and muscles of the shoulder girdle, especially the m. latissimus dorsi. Posterior to the 10th vertebra no differentiation of the m. dorsalis trunci can, as yet, be observed. The foremost of the mm. inter-

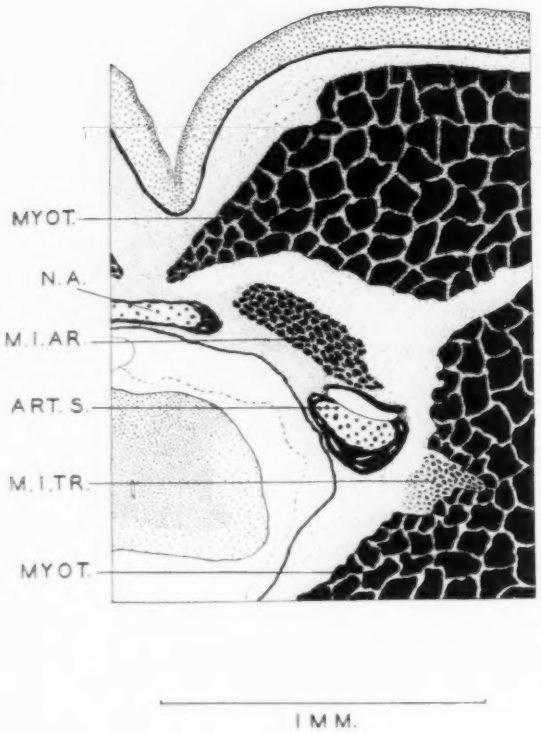

Fig. 14. Transverse section through the anlage of the m. intertransversarius. Stage 58. *MYOT.* myotome (m. dorsalis trunci); *N.A.* neural arch; *M.I.AR.* m. interarcualis; *ART.S.* articulation surface; *M.I.TR.* m. intertransversarius; *MYOC.* myocomma.

transversarii, developing between consecutive transverse processes of the vertebrae, are represented by a muscle cord stretching between the postero-dorsal surface of the otico-occipital complex and the first rib. This muscle is designated as the m. intertransversarius capitis superior to distinguish it from a similar muscle, the m. intertransversarius capitis inferior, which also takes origin from the rib and inserts itself onto the ventral surface of the above-mentioned complex. There is no doubt that the mm. intertransversarii arise from the myotomes. In fact, these muscles are the best proof that the secondary muscles develop by means of the disintegration and rebuilding of muscle fibres belonging to the primary group. The developing muscles appear in trough-like excavations on the medial sides of the myotomes. In younger stages the positions of these excavations are occupied by fibres of the myotomes, but in this stage the excavations are filled with developing muscle cells (fig. 14). The process of transformation is probably effected by amoeboid cells derived from "mesenchyme".

In the following stages (59 and 60) the ventro-medial portion of trunk myotome III has gained complete independence of the dorsal portion to which it was still attached in stage 57. It appears as a muscle cord lying lateral to

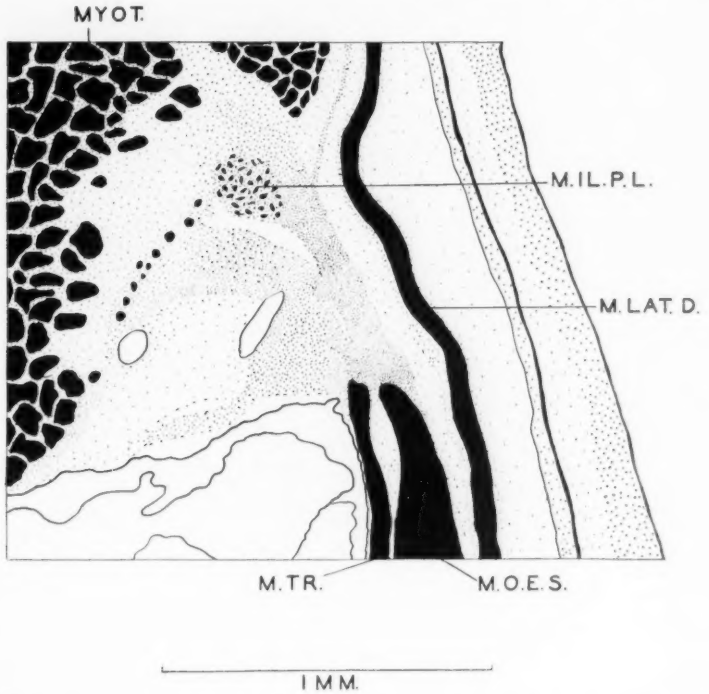

Fig. 15. Transverse section through the anlage of the m. ileolumbalis, pars lateralis. Stage 62. *M.IL.P.L.* m. ileolumbalis, pars lateralis; *M.LAT.D.* m. latissimus dorsi; *M.TR.* m. transversus abd.; *M.O.E.S.* m. obliquus abd. externus superficialis; *MYOT.* myotome (m. dorsalis trunci).

the centra of the atlas and 2nd vertebra and ventral to the transverse process of the latter and the first rib. The fascia dorsalis constitutes a thick connective tissue plate on the dorsal side of the m. dorsalis trunci. Dorso-medially, where it is known as the fascia intermuscularis, it stretches downwards, reaching the dorsal surfaces of the vertebral arches in the medio-ventral line (fig. 5). There are no mm. intertransversarii or mm. interarcuales posterior to the 9th vertebra, and there are still no indications of further differentiation of the m. dorsalis trunci. The m. interarcualis between the 9th and 10th vertebrae is indistinguishable from the dorso-medial fibres of the m. dorsalis trunci. The 10th vertebra is, of course, part of the urostyle.

In the next two stages (61 and 62) two new muscles derived from the m. dorsalis trunci can be observed. The foremost of these, known as the m. ileolumbalis, pars lateralis, develops in front of the anterior tip of the ilium, stretches in an anterior direction on the medio-dorsal side of the m. transversus abd. and underlies the m. dorsalis trunci. Proliferations from the latero-ventral side of the m. dorsalis trunci (actually that part which constitutes the

VOL. 34 1953

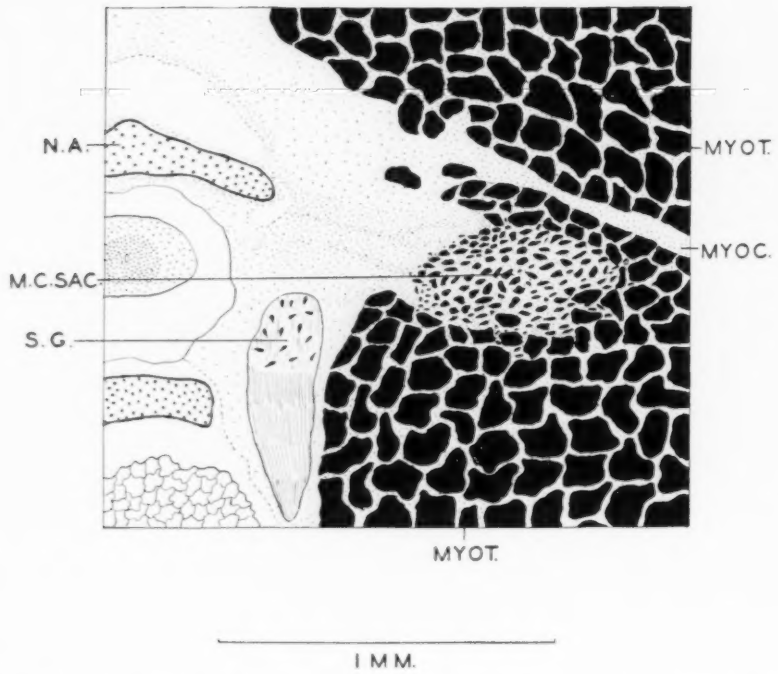

Fig. 16. Transverse section through the postero-medial part of the trunk to show the anlage of the m. coccygeo-sacralis. Stage 62. *N.A.* neural arch; *M.C.SAC.* m. coccygeo-sacralis; *S.G.* spinal ganglion; *MYOT.* myotome (m. dorsalis trunci); *MYOC.* myocomma.

m. ileolumbalis, pars medialis of the adult) and probably some intermediate mesenchyme-like cells contribute to the formation of this muscle (fig. 15). During the last few stages of metamorphosis (63—65) the pars lateralis expands, and its origo on the ventral side of the anterior tip of the ilial wing can be clearly observed. It reaches cranially to approximately the level of the 3rd vertebra, attaching itself to the aponeurosis on the ventral side of the dorsal myomeres. As is the case with all the components of the dorsal musculature its fibres run longitudinally. The pars lateralis of the m. ileolumbalis overlies the longitudinal fibres of the m. transversus abd.

The second new muscle, developing during stage 61, the m. coccygeo-sacralis, is a caudad continuation of the mm. intertransversarii and develops in exactly the same position and in the same manner as the latter (fig. 16). Anteriorly it is inserted onto the postero-ventral surface of the transverse process of the 9th vertebra. Owing to the fusion of the sacral vertebra to the urostyle (composed of material derived from three vertebral segments, [Smit, in press]) and the absence of transverse processes from the latter, the m. coccygo-sacralis is attached to the lateral surface of the urostyle. In the subsequent stages this

muscle becomes much more conspicuous and covers the medial portion of the m. dorsalis trunci ventral to the transverse process of the 9th vertebra. This particular ventral part of the m. dorsalis trunci is known as the m. coccygeo-iliacus in the adult. Its formation, or rather, its differentiation as a separate muscle independent of the m. dorsalis trunci, is partly due to the development of the extensive transverse process of the sacral vertebra. During metamorphosis axial mesenchyme cells penetrate the muscle tissue along a horizontal line at the level of the transverse process, and they constitute a thick connective tissue layer stretching from the 9th vertebra to the medial side of the ilial wing. Owing to its breadth the process divides the m. dorsalis trunci into a dorsal and a ventral portion. Behind this process the division is maintained by the presence of the m. coccygeo-sacralis. Behind the latter, however, there is, at this stage, no dividing tissue between the m. coccygeo-iliacus and the m. dorsalis trunci (Stage 64). Anteriorly the fibres of the m. coccygeo-iliacus are inserted onto the medial surface of the distal part of the ilial wing. Owing to the fact that the m. coccygeo-iliacus represents the ventral portions of two myomeres, a medial and lateral portion can be distinguished, a myocomma still separating them at this stage. The front border of this muscle is also formed by a myocomma between myotomes VIII and IX. The m. coccygeo-iliacus is completely covered laterally by the enormously developed m. iliacus externus. It must be stressed that the origin of the m. coccygeo-iliacus is by no means the same as, for instance, that of the m. coccygeo-sacralis. It is part of the m. dorsalis trunci, separated from it only by means of developing skeletal and connective tissue structures. No intermediate cells contribute towards its formation, the muscle itself representing part of the primary dorsal musculature.

When reviewing the degree of development of the dorsal somatic musculature of the trunk at the stage immediately before transformation into the young adult (Stage 64) it becomes evident that all the muscles of this latter stage are already present. The m. dorsalis trunci covers the dorsal and lateral surfaces of the vertebral column. Posteriorly it is still continued into the tail, and anteriorly it overlaps the lateral surfaces of the otic and occipital regions. There are, at this stage, indications that the ventral part of the m. dorsalis trunci, underlying the transverse processes and reaching from the 2nd to the 9th vertebrae, is being separated from the dorsal part by means of a horizontal connective tissue layer (fascia lumbodorsalis) penetrating the muscle mass. This layer stretches out along the level of the ribs and transverse processes, joining the ventral parts of the original myocommata. The new muscle, the m. ileolumbalis, pars medialis, is thus constructed by means of the union of the ventral portions of the trunk myotomes IV to VIII, the myocommata still being present. At this stage a few remaining fibres of trunk myotome III stretch forwards from the anterior part of the m.i., pars medialis. This latter muscle thus differentiates from the m. dorsalis trunci in more or less the same manner as its posterior

VOL.
34
1953

continuation, the m. coccygeo-iliacus. The remaining dorsal part of the m. dorsalis trunci, after the separation of these muscles, is known as the m. longissimus dorsi.

The mm. interarcuales are represented anteriorly by fibres covering the occipital region above the foramen magnum, its fibres being in close association with the medio-dorsal part of the m. longissimus dorsi. They stretch backwards from the atlas, joining the consecutive vertebral arches. There are no distinguishable representatives of these muscles posterior to the sacral vertebra. The mm. intertransversarii stretch between consecutive transverse processes, including those of the 2nd and 9th vertebrae. Anteriorly they are represented by a m. intertransversarius capitis superior and inferior, stretching from the first rib to the dorsal and ventral aspects of the occipitalis lateralis respectively. This series is continued backwards as the m. coccygeo-sacralis, taking origin from the ventral surface of the transverse process of the 9th vertebra and inserted onto the anterior part of the urostyle. The m. ileolumbalis, pars lateralis takes origin from the anterior tip of the ilial wing and inserts itself onto the tip of the 3rd rib corresponding to the transverse process of the 4th vertebra.. The last muscle to be mentioned is the m. coccygeo-iliacus, a separated off portion of the m. dorsalis trunci, inserted onto the lateral surface of the urostyle and attaching itself to the medial aspect of the anterior part of the ilial wing (figs. 28 and 29).

VOL
34
195

2. The ventral somatic musculature

The metamorphosis of the ventral musculature is initiated by new developing secondary muscles in close connection with the m. rectus abdominis. Superficial proliferating cells, arising from the previously mentioned slender ventrolateral projection of the m. rectus abd., forms the anlage of a muscle which will, during later stages, insert itself onto the dorsal aspect of the procoracoid (fig. 17). This anlage is situated in the region anterior to the heart. Posterior to the shoulder girdle, the anlage of another superficial layer can be observed next to almost the entire lateral surface of the m. rectus abd. (fig. 12). It takes its origin from the m. rectus abd. in the same manner as do all the other secondary muscles, i.e. from their corresponding primary muscles. The major part of this muscle, the m. rectus abdominis superficialis, lies contiguous to the original m. rectus (m. rectus abdominis profundus) and is separated from it by means of its perimysium. It is also very probable that intermediate amoeboid cells aid in the transformation of the fibres of the primary muscle and the formation of the new secondary derivative.

The m. obliquus abd. externus superficialis and the m. transversus abd. have not, as yet, extended very far ventrally. Loose fibres of the primary m. obliquus abd., some of them still joining those of its derivatives, are visible between the

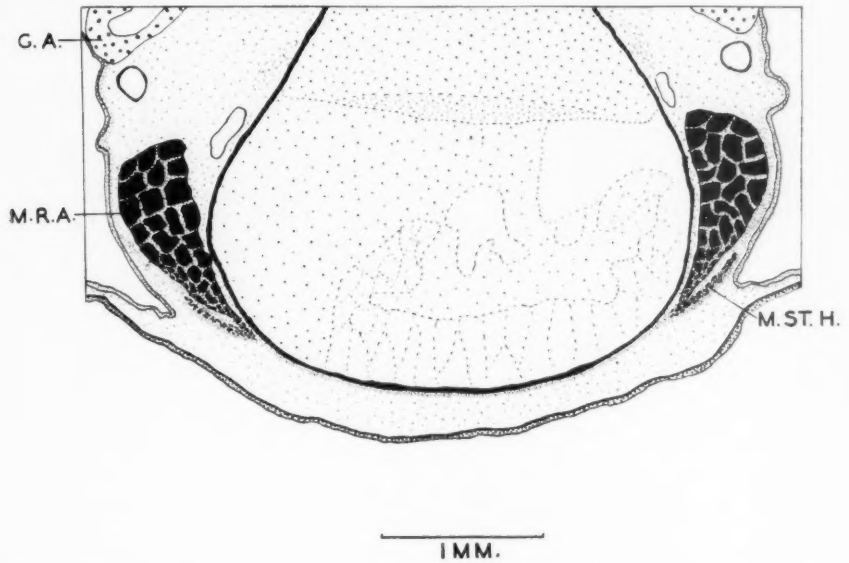

Fig. 17. Transverse section through the anterior region of the trunk to show the anlage of the m. sternohyoideus, pars lateralis. Stage 58. *G.A.* last gill arch; *M.R.A.* m. rectus abdominis; *M.ST.H.* m. sternohyoideus.

latter two muscles. Anteriorly the foremost fibres of the m. transversus abd., running in a longitudinal direction, insert themselves into a connective tissue plate on the medial side of the shoulder girdle.

The later stages of metamorphosis are characterized by the development of those superficial layers which overlie the m. rectus abd. profundus. Immediately behind the middle portion of the heart another layer of superficial fibres separates itself off from the ventro-lateral side of the rectus abd. profundus and becomes attached to the coracoid by means of a thick connective tissue strand (fig. 18). During subsequent stages of metamorphosis these fibres join those of the ventral projection (arising from the m. rectus abd. profundus, fig. 17) anterior to it and constitute a medio-ventral muscle plate, the m. sternohyoideus, which inserts onto the dorsal and medial surfaces of the procoracoid cartilages and the dorsal surface of the processus epicoracoideus. This muscle is almost entirely separated off from the m. rectus abd. by means of its perimysium. Its dorsal portion overlies the ventral part of the m. rectus abd. Posteriorly the m. sternohyoideus extends backwards to insert onto the dorsal surface of the developing sternum. In this region there is no close relation between the m. sternohyoideus and the m. rectus abd. The formation of this secondary muscle is thus effected by joining of fibres from two areas on the lateral side of the m. rectus abd. During the latest stages of metamorphosis, however, the anterior part of the m. sternohyoideus joins the fibres of the m. rectus abd. Only that part

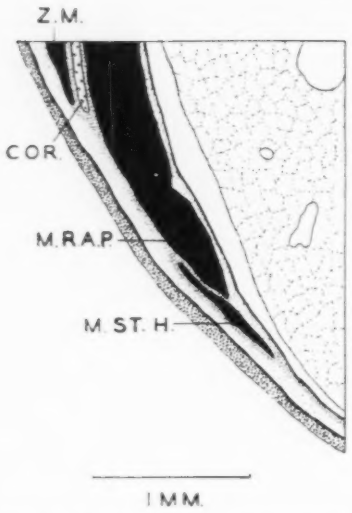

Fig. 18. Transverse section through the anlage of the pars medialis of the m. sternohyoideus. Stage 60. *Z.M.* zonal muscle; *COR.* coracoid; *M.R.A.P.* m. rectus abdominis profundus; *M.ST.H.* m. sternohyoideus.

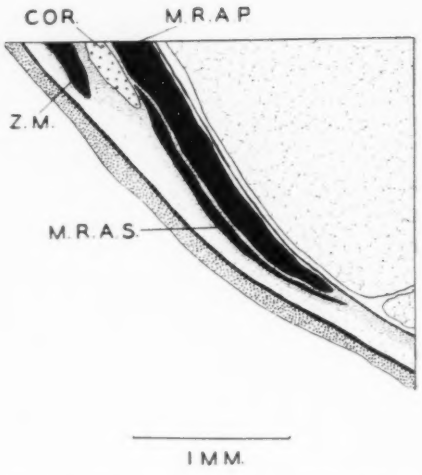

Fig. 19. Transverse section through the m. rectus abd. profundus and m. rectus abd. superficialis. Stage 58. *COR.* coracoid; *M.R.A.P.* m. rectus abdominis profundus; *Z.M.* zonal muscle; *M.R.A.S.* m. rectus abdominis superficialis.

of the former overlying the posterior surface of the processus epicoracoideus and the sternum, constitutes an independent muscle.

During this period the m. rectus abdominis superficialis develops into a thick muscle plate on the outer side of the m.r.abd. profundus. The anterior lateral surface of the former is completely covered by a thick connective tissue layer stretching ventro-mediad from the coracoid (fig. 19). In the medio-ventral line this connective tissue is designated as the linea alba. This part of the linea alba forms the mother tissue from which the sternum develops (DE VILLIERS, 1922, 1924), and, as can be expected, the m. rectus abd. superficialis attaches itself to this skeletal structure. During the later stages of metamorphosis it inserts onto its postero-dorsal surface as well as onto the edges of the lateral wings. A striking feature of the m. rectus abd. superficialis during metamorphosis is its relation relative to the m. rectus abd. profundus. The beginning of metamorphosis shows the former lying practically contiguous to the latter, but they very soon become more and more separated from each other so that large open spaces are formed between them. Towards the end of metamorphosis, however, the m.r.abd. superficialis tends to renew its intimate association with the profundus, producing a state of affairs which simulates the condition obtained during the first stages of its development.

Throughout metamorphosis the m. rectus abd. profundus remains a mas-

sively built muscle, attaching to the developing skeletal structures in its vicinity. The fibres of the primary m. obliquus abd. gradually disintegrate in inverse proportion to the degree of development of the m. obliquus abd. externus superficialis and m. transversus abd. It can be readily assumed that, at the end of metamorphosis, the remaining part of the primary ventral musculature is represented only by the m. rectus abdominis profundus.

The most anterior fibres of the m. transversus abd. run longitudinally and insert into an aponeurosis on the latero-ventral side of dorsal myotome IV, in the approximate vicinity of the ventral nerve supplying the fore-limb. During the early stages this longitudinal fibre plate is connected to the dorsal edge of the m. rectus abd. by means of a connective tissue layer. The remnants of the primary m. obliquus abd. which were present between the m. obliquus abd. externus superficialis and the m. transversus abd. have disappeared, the m. transversus now covering the dorso-lateral surface of the m. rectus abd. Posteriorly the m. transversus abd. takes origin from the outer surface of the ilial wing, the aponeurosis of the m. iliacus externus and the front border of the m. glutaeus magnus.

As is the case in the m. transversus abd. the m. obliquus abd. externus superficialis gradually increases in size during the metamorphic stages. Anteriorly its fibres are inserted onto the posterior part of the developing suprascapula, the foremost fibres running between the latter and the lateral side of the coracoid. Behind the shoulder girdle it is contiguous to the m. transversus abd. and, like this muscle, inserts into the aponeurosis of the ventro-lateral portion of the dorsal myomeres. Posteriorly the m. obliquus abd. externus superficialis, together with the m. transversus abd., originate from the lateral surface of the tip of the ilial wing, the aponeurosis of the m. iliacus externus and the front border of the m. glutaeus magnus of the hind limb. On the lateral side the m. obliquus externus is covered by the m. latissimus dorsi and the pars abdominalis of the m. pectoralis.

Briefly the topography of the ventral muscles of the trunk at the end of metamorphosis is as follows:—The greater part of the ventral and lateral covering of the abdominal cavity is represented by the m. rectus abdominis profundus. Anteriorly it inserts onto the posterior part of the hyoid, the pericardial sac, the coracoid and the latero-dorsal surface of the sternum. Posteriorly it stretches backwards and takes origin from the dorsal surface of the epipubis and the front margin of the m. sartorius of the hind limb. In the ventro-median line it lies against the linea alba. The m. rectus abdominis superficialis overlies the m.r.abd. profundus on its ventral and ventro-lateral sides over an area approximately constituting the middle third of the trunk. The m. sternohyoideus is intimately associated with the m. rectus abdominis anteriorly, and both insert onto the posterior aspect of the hyoid. Posteriorly it constitutes a separate muscle, overlying the epicoracoid and originating from the medio-dorsal sur-

face of the sternum. The m. transversus abd. covers the medio-dorsal surface of the abdominal cavity and lies dorsally to the m. rectus abd. profundus. In front, the fibres of the m. rectus abd. profundus assist the m. transversus abd. in covering the lateral portion of the abdominal cavity. Caudally the m. transversus abd. takes origin from the ilial wing, the aponeurosis of the m. iliacus externus and the front margin of the m. glutaeus magnus. The m. obliquus abd. externus superficialis overlying the m. transversus abd., attaches itself to the suprascapula, the coracoid and aponeuroses of the zonal muscles. Posteriorly it takes origin from the same structures as the m. transversus abd. The striking features at this stage are the extensively developed m. obliquus abd. externus superficialis, and to a smaller extent, the m. transversus abd. To be noted also is the presence of a m. rectus abdominis superficialis and the absence of the primary m. obliquus abd.

3. *Zonal muscles covering the trunk*

During metamorphosis numerous muscles develop in connection with the pectoral and pelvic girdles. Most of these, except those mentioned in the description of the pre-metamorphic stages, are of minor importance as far as the covering of the trunk is concerned. The m. latissimis dorsi as well as the m. pectoralis, pars abdominialis extend in a posterior direction, almost completely covering the outer surfaces of the true muscles of the trunk. The m. iliacus externus expands enormously so that it almost entirely surrounds the ilial wing. A more detailed description of these muscles will be given in the next stage.

VOL. 34 1953

C. THE EARLY POST-METAMORPHIC STAGE

When examining the muscles of the trunk in a young adult, it becomes evident that the condition of the musculature at this stage is essentially that found in the older adult. During post-metamorphic life there is, however, a definite tendency for the muscles to become more intimately related with one another (see Discussion). To facilitate the comparison with the adult, a detailed description of the somatic muscles of the early post-metamorphic stage (Stage 66) is necessary.

1. *Muscles of the vertebral column*

These include all the muscles which are partially or entirely derived from the m. dorsalis trunci.

M. longissimus dorsi (figs. 22, 23 and 26)

This muscle takes origin from approximately the entire lateral and dorsolateral surfaces of the urostyle. From its most posterior point of origin it gradu-

ally broadens, its lateral part finding attachment to the dorsal surface of the extensive transverse process of the 9th vertebra. Anterior to this process it slightly narrows down, at the same time extending in a cranial direction, dorsally across the transverse processes and neural arches of the vertebrae and the ribs fused to the diapophyses of the 2nd, 3rd, and 4th vertebrae. Between the consecutive neural arches and the transverse processes it respectively covers the mm. interarcuales and mm. intertransversarii. In the interspaces between the latter it forms a dorsal covering to the m. ileolumbalis, a thick connective tissue layer separating them from each other. The lateral portions of these two muscles, however, are not yet sharply demarcated. In the region, of the transverse process of the 2nd vertebra (the atlas having no transverse process) the lateral fibres stretch forwards to insert onto the dorso-lateral surface of the prooticoccipital complex. In the region of the atlas the medial fibres join those of the m. interarcualis capitis (the foremost interarcual muscle) and insert onto the dorsal surface of the occipital above the foramen magnum. The whole muscle is divided into 9 segments by means of 8 myocommata, representing those originally occurring between the consecutive myotomes III to XI. The foremost segment (myomere) constitutes the fused dorsal portions of trunk myotomes II and III. Owing to the zig-zag course of the myocommata the myomeres overlap each other, making it possible to see sections of 2 to 3 segments in one cross section (fig. 20). All the fibres of the longissimus dorsi run in a longitudinal direction, mainly from myocomma to myocomma. Only the medial, the ventral and the most anterior fibres are inserted onto skeletal structures.

M. ileolumbalis (Hoffmann)

This is a compound muscle representing a portion of the original m. dorsalis trunci and a secondary muscle strip derived from it, respectively known as the m. ileolumbalis, pars medialis and pars lateralis. In this stage these two muscles are completely separate.

The pars medialis

(figs. 21 and 23) underlies the transverse processes of the 2nd to the 9th vertebrae and covers the lateral surfaces of their centra. Postero-laterally it takes origin from the inner surface of the ilial wing and postero-medially from the front margin of the transverse process of the sacral vertebra. Its hindmost fibres are dorsally covered by the m. coccygeo-sacralis. Lateral fibres of the pars medialis are still intimately associated with those of the m. longissimus dorsi. The muscle is divided into 5 segments, the transverse myosepta representing the ventral parts of the original myocommata. From the transverse process of the 9th vertebra backwards, this muscle is designated as the m. coccygeo-iliacus. It is separated from the m. ileolumbalis by a myocomma. The

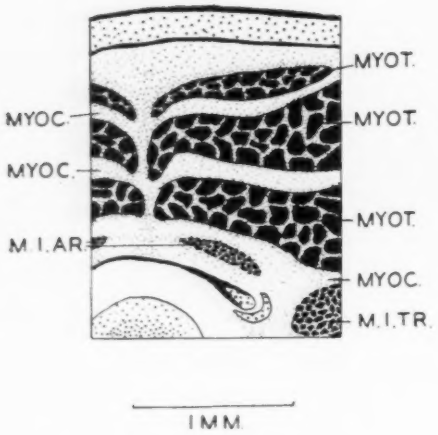

Fig. 20. Transverse section through the dorso-medial portion of the trunk to show the number of myotomes visible in one section. Stage 66. *MYOT.* myotome; *MYOC.* myocomma; *M.I.AR.* m. interarcualis; *M.I.TR.* m. intertransversarius.

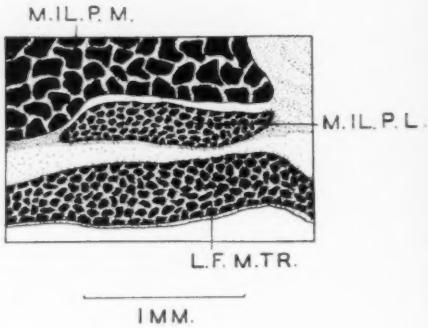

Fig. 21. Transverse section through the m. ileolumbalis, pars lateralis. Stage 66. *M.IL.P.M.* m. ileolumbalis, pars medialis; *M.IL.P.L.* m. ileolumbalis, pars lateralis; *L.F.M.TR.* longitudinal fibres of the m. transversus abd.

VOL. 34 1953

m. coccygeo-iliacus and the m.i., pars medialis have similar relations to the m. longissimus dorsi.

The pars lateralis

(figs. 21, 26 and 29) is a secondary muscle taking origin from the outer surface of the cartilaginous anterior tip of the ilial wing (fig. 26), close to the attachment of the m. iliacus externus. From a position dorso-lateral to the m.i., pars medialis it stretches in a cranial and slightly ventro-medial direction to insert into the myocomma, corresponding to the 5th vertebra, and the distal part of the 3rd rib, corresponding to the 4th vertebra. The most anterior fibres of the m.i., pars lateralis lie squeezed in between the ventral and dorsal surfaces of the m.i., pars medialis and the longitudinal fibres of the m. transversus abd. respectively (fig. 21). On the ventral aspect of the m.i., pars medialis, these fibres insert into an aponeurosis attached, to the centrum of the 4th vertebra.

M. coccygeo-iliacus (fig. 22)

This represents the hinder part of the ventral portion of the m. dorsalis trunci. The fibres of this muscle take origin from the greater part of the lateral surface of the urostyle, stretch out in an antero-lateral direction, and insert onto the medial surface of the distal portion of the ilium. The dorsal surface of its anterior half is covered by the m. coccygeo-sacralis, which prevents its insertion onto the ventral face of the transverse process of the sacral vertebra.

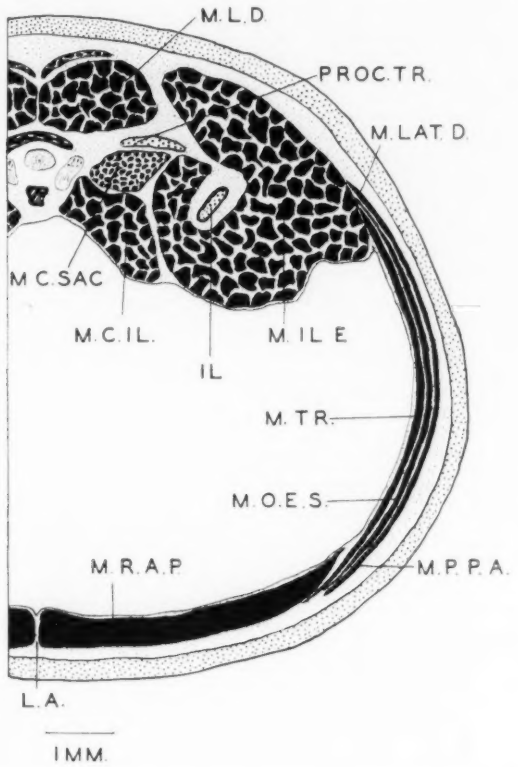

Fig. 22. Transverse section through the musculature of the trunk in the region of the transverse process of the 9th vertebra. Stage 66. *M.L.D.* m. longissimus dorsi; *PROC.TR.* transverse process of the sacral vertebra; *M.LAT.D.* m. latissimus dorsi; *M.P.P.A.* m. pectoralis, pars abdominalis; *L.A.* linea alba; *M.R.A.P.* m. rectus abdominis profundus; *M.O.E.S.* m. obliquus abdominis externus superficialis; *M.TR.* m. transversus abdominis; *M.IL.E.* m. iliacus externus; *IL.* ilium; *M.C.IL.* m. coccygeo-iliacus; *M.C.SAC.* m. coccygeo-sacralis.

Although closely associated with each other, these two muscles do not fuse. The lateral border of the m. coccygeo-iliacus is apposed to the inner face of the massive m. iliacus externus. "Transverse myosepta", representing remnants of the original myocommata, can still be distinguished.

Mm. intertransversarii (figs. 20 and 23)

These are "short" muscles of the vertebral column extending between consecutive transverse processes. The most anteriorly situated intertransversarius is known as the *m. intertransversarius capitis superior.* It takes origin from the tip of the first rib, extends medio-dorsal, and inserts onto the occipital and the dorsal surface of the prootic-occipital complex. This muscle constitutes the first m. intertransversarius as it is derived from trunk myotome II. The second

m. intertransversarius, the *m. intertransversarius capitis inferior*, corresponding to trunk myotome III, takes origin from the ventral surface of the same rib but, cranially, its fibres are inserted onto the ventral aspect of the prootic-occipital complex. The rest of the mm. intertransversarii can all be distinguished as separate muscles, the last one connecting the transverse processes of the 8th and 9th vertebrae. Between the 3rd and the 4th vertebrae there are two mm. intertransversarii: a median and a lateral one. The latter consists of only a few fibres, which stretch between the distal ends of the 2nd and 3rd ribs. This muscle cannot be regarded as a true m. intertransversarius because it develops much later during ontogeny and merely represents a separated off portion of the m. longissimus dorsi.

M. coccygeo-sacralis (fig. 22)

This muscle can be regarded as a caudad continuation of the intertransversarius series. It takes origin from the lateral surface of the anterior two-thirds of the urostyle immediately above the attachment of the m. coccygeo-iliacus. It stretches cranially and slightly outwards, its lateral fibres inserting into the medial surface of the ilial wing by means of a tendinous connective tissue strip. The bulk of the muscle, however, is inserted onto the ventral surface of the extensive transverse process of the sacral vertebra. As is the case with the m. coccygeo-iliacus the lateral side of this muscle is covered by the m. iliacus externus.

VOL. 34 1953

Mm. interarcuales (= interspinales, intercrurales) (figs. 20 and 23)

These also are a series of "short" muscles stretching between consecutive neural arches of the vertebrae. The foremost of these, the *m. interarcualis capitis*, stretches from the neural arch of the atlas to insert onto the dorsal aspect of the exoccipital. Its fibres cannot be distinguished from those of the dorso-medial part of the m. longissimus dorsi. The fibres of the second and third mm. interarcuales, running between the 1st and 2nd and the 2nd and 3rd vertebrae respectively, are not intimately associated with the m. longissimus dorsi. The last six mm. interarcuales, the hindmost of which runs between the 8th and 9th vertebrae, are all intimately associated with the m. longissimus dorsi. Apart from the fibres which stretched between the 9th and 10th vertebrae, during earlier larval stages, this series of muscles is not represented behind the sacral vertebra. These fibres have fused with the m. longissimus dorsi and at this stage are not recognizable as such.

2. *Muscles of the abdominal wall*

M. rectus abdominis profundus (figs. 22, 23 and 24)

This muscle takes origin from the latero-dorsal surface of the epipubis (fig. 24) and from an aponeurosis on the front margin of the m. sartorius of the

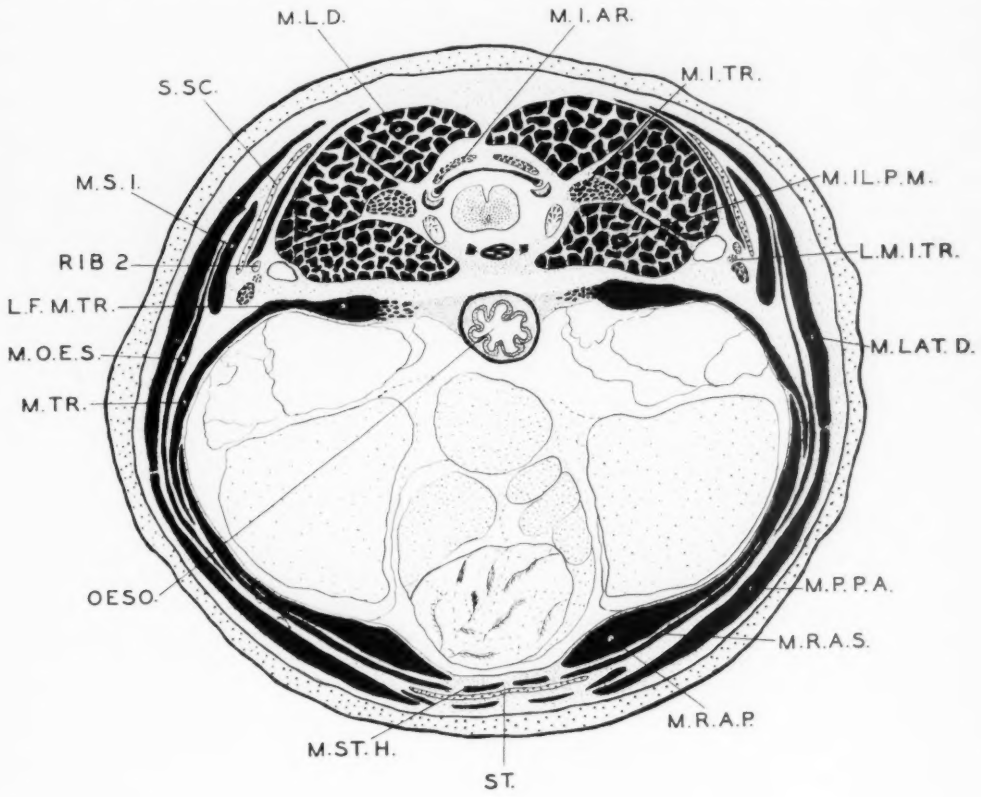

Fig. 23. Transverse section through the anterior part of the trunk in the region of the sternum. Stage 66. *M.I.AR.* m. interarcualis; *M.I.TR.* m. intertransversarius; *M.IL.P.M.* m. ileolumbalis, pars medialis; *L.M.I.TR.* lateral m. intertransversarius; *M.LAT.D.* m. latissimus dorsi; *M.P.P.A.* m. pectoralis, pars abdominalis; *M.R.A.S.* m. rectus abdominis superficialis; *M.R.A.P.* m. rectus abdominis profundus; *ST.* sternum; *M.ST.H.* m. sternohyoideus; *OESO.* oesophagus; *M.TR.* m. transversus abdominis; *M.O.E.S.* m. obliquus abdominis externus superficialis; *L.F.M.TR.* longitudinal fibres of the m. transversus abdominis; *M.S.I.* m. serratus inferior; *S.SC.* suprascapula; *M.L.D.* m. longissimus dorsi.

pelvic girdle. The linea alba, separating the ventro-medial ends of the two rectus muscles, is a broad connective tissue plate in the region of the epipubis. Immediately behind the most posterior attachment of the m. rectus abd. profundus the linea alba is represented by a thick connective tissue strip consisting of spindle-shaped cells. This part of the linea alba serves as attachment for the m. epipubicus along the postero-dorsal surface of the epipubis. Anterior to the epipubis the linea alba is reduced to a very thin plate of connective tissue still separating the rectus muscles in the ventro-median line (fig. 22).

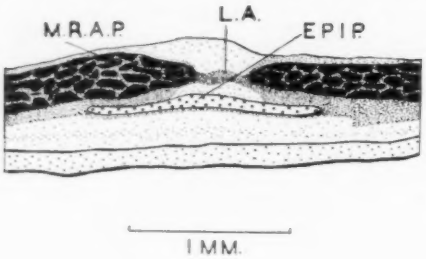

Fig. 24. Transverse section through the epipubis to show the origo of the m. rectus abdominis. Stage 66. *M.R.A.P.* m. rectus abdominis profundus; *L.A.* linea alba; *EPIP.* epipubis.

The ventral half of the middle portion of the m. rectus abd. profundus is partly covered by the m. rectus abd. superficialis, whereas the dorsal part is over its entire length overlapped by the m. transversus abd. and m. obliquus abd. externus superficialis (fig. 23). Upon approaching the shoulder girdle the m. transversus abd. is gradually reduced to a number of dorsally situated longitudinal fibres. Pari passu with this reduction, the m.r.abd. profundus reaches more dorsad so that their fibres are almost contiguous. Ventrally the rectus profundus inserts onto the postero-latero-dorsal surface of the sternum in front of the insertion of the rectus superficialis. The medio-dorsal surface of the sternum is occupied by the insertion of the m. sternohyoideus, the lateral fibres of which join those of the m. rectus abd. profundus in front of the coracoid. The profundus extends forwards, attaches to the pericardium and is inserted onto the hyoid.

M. rectus abdominis superficialis (figs 23 and 25)

This muscle stretches from approximately the level of the anterior tip of the ilium to the posterior region of the sternum. The whole muscle approaches the m. rectus abd. profundus much closer than it did during the preceding stages and is practically contiguous to it. Its hindmost fibres are indistinguishable from those of the m. rectus abd. profundus. In the medio-ventral line the right and left superficiales lie close to each other, whereas the profundus muscles are separated from each other by a broad linea alba. The dorsal fibres of the m.r.abd. superficialis almost reach those of the m. transversus abd. and m. obliquus abd. externus superficialis, the entire m. r. profundus being thus covered externally. Anteriorly the rectus superficialis inserts onto the dorsal surface of the sternum where its lateral fibres are intimately associated with those of the rectus profundus (fig. 23).

M. sternohyoideus (fig. 23)

It takes origin from the medio-dorsal surface of the sternum immediately anterior to the insertion of the m. rectus abd. superficialis and medio-ventral to the margin of the m. rectus abd. profundus. The muscle stretches forwards across the dorsal surfaces of the processus epicoracoideus and the procoracoid

VOL. 34 1953

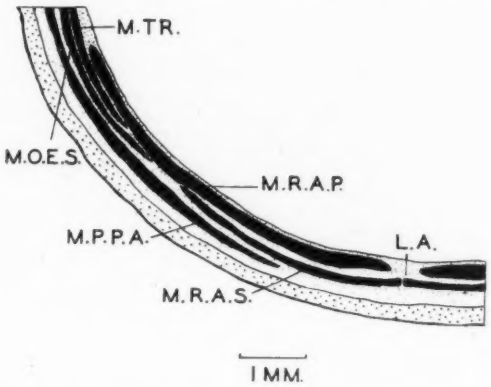

Fig. 25. Transverse section through the muscles of the latero-ventral part of the trunk. Stage 66. *M. TR.* m. transversus abdominis; *M.R.A.P.* m. rectus abdominis profundus; *L.A.* linea alba; *M.O.E.S.* m. obliquus abd. externus superficialis; *M.P.P.A.* m. pectoralis, pars abdominalis; *M.R.A.S.* m. rectus abdominis superficialis.

and inserts onto the hyoid in close proximity to the m. rectus profundus. The lateral fibres of the m. sternohyoideus join those of the m. rectus abd. profundus immediately posterior to the coracoid-epicoracoid junction.

M. obliquus abdominis externus superficialis (figs. 22, 23 and 26)

The external oblique muscle originates from the fascia dorsalis and the aponeuroses of certain muscles of the hind limb. Antero-laterally it takes origin from the lateral surface of the tip of the ilial wing. The whole muscle extends forwards, the ventral portion ending in an aponeurosis, whereas the slender dorsal division covers the postero-dorsal surface of the suprascapula. This latter portion (pars scapularis) inserts into an aponeurosis between the m. latissimus dorsi and the m. serratus inferior. Except for its hindmost part the m. obliquus abd. externus is completely covered by the m. latissimus dorsi and the pars abdominalis of the m. pectoralis.

M. transversus abdominis (figs. 22, 23 and 26)

Similar to the m. obliquus abd. externus superficialis, the m. transversus abd. takes origin from the fascia dorsalis and aponeuroses of the hind limb muscles. These hindmost portions of the m. obliquus abd. externus and of the m. transversus abd. are intimately associated with each other, the latter stretching somewhat further backwards than the former. The postero-dorsal portions of the m. transversus abd., m. obliquus abd. externus and m. latissimus dorsi overlap the latero-dorsal surface of the m. iliacus externus. The ventral part of the m. transversus overlies the dorso-lateral surface of the m. rectus abd. profundus. The dorsal longitudinal fibres of the m. transversus abd. originate from the ventral surface of the tip of the ilial wing between the medial and

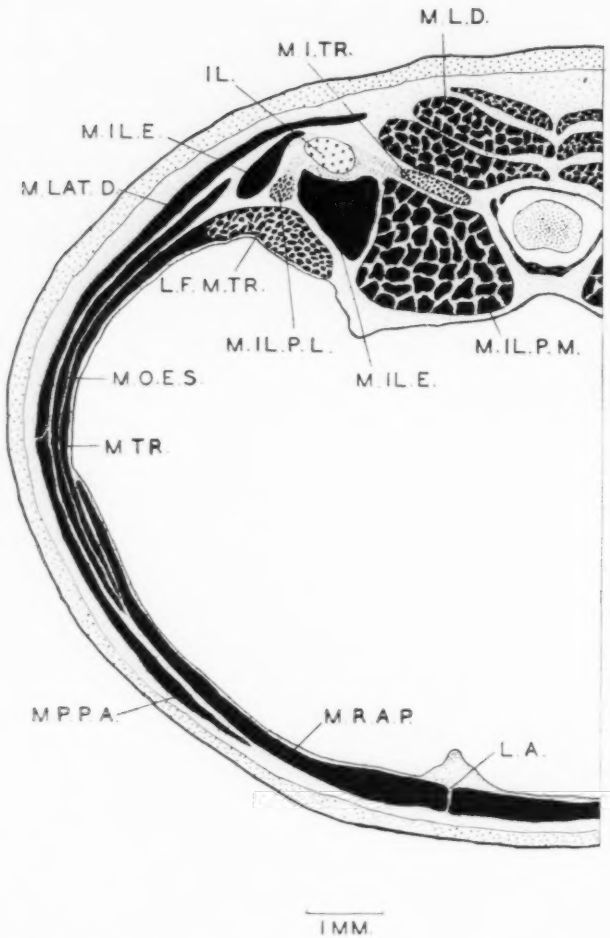

Fig. 26. Transverse section through the trunk in the region of the ilial wing. Stage 66. *M.L.D.* m. longissimus dorsi; *M.I.TR.* m. intertransversarius; *IL.* ilium; *M.IL.E.* m. iliacus externus; *M.LAT.D.* m. latissimus dorsi; *M.P.P.A.* m. pectoralis, pars abdominalis; *L.A.* linea alba; *M.R.A.P.* m. rectus abd. profundus; *M.TR.* m. transversus abd.; *M.O.E.S* m. obliquus abd. externus superficialis; *L.F.M.TR.* longitudinal fibres of the m. transversus; *M.IL.P.L.* m. ileolumbalis, pars lateralis; *M.IL.E.* m. iliacus externus; *M.IL.P.M.* m. ileolumbalis, pars medialis.

lateral portions of the m. iliacus externus. Immediately anterior to this attachment these fibres are joined to the transverse fibres of the m. transversus abd. The horizontally placed fibres shift medially and proceed ventrad to the medial portion of the m. iliacus externus. Anterior to the insertion of the latter they are covered dorsally by the pars medialis and pars lateralis of the m. ileolumbalis. In this region the m. transversus abd. forms a dorso-lateral covering for the

VOL. 34 1953

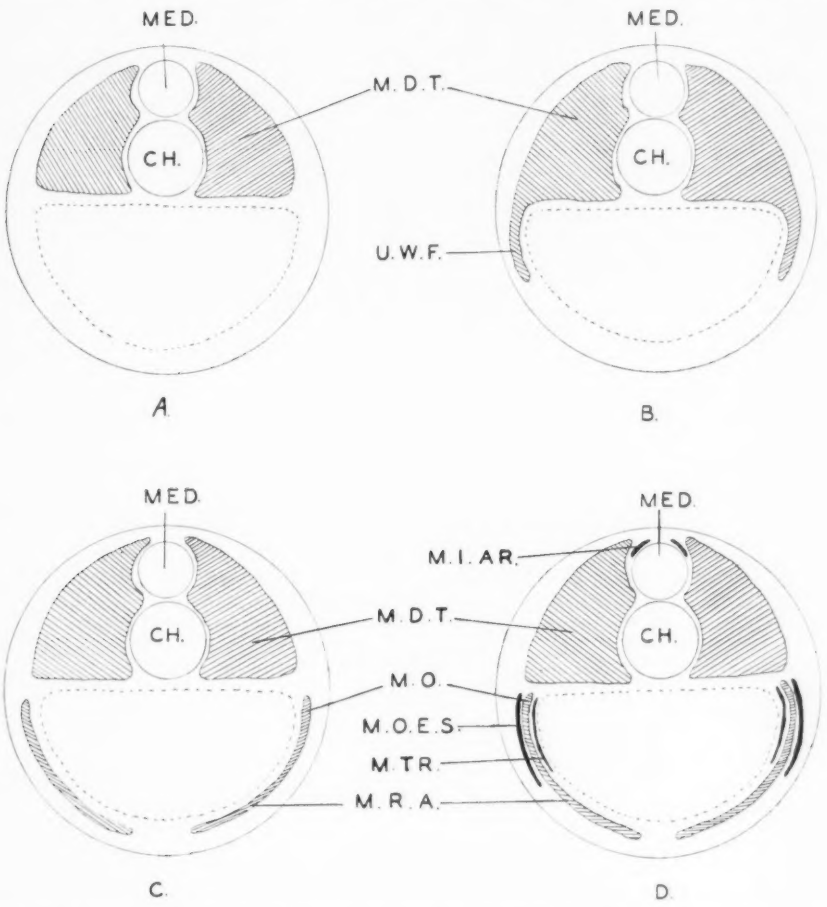

Fig. 27. Schematic diagrams of transverse sections through the trunk. Consecutive stages of the pre-metamorphic period. Secondary muscles in black, primary muscles oblique lines.

A. The myotome. B. The formation of the "Urwirbelfortsatz". C. The detachment of the ventral musculature. D. The anlagen of the first secondary muscles. *MED.* medulla spinalis; *CH.* chorda dorsalis; *M.D.T.* m. dorsalis trunci; *U.W.F.* "Urwirbelfortsatz"; *M.I.AR.* m. interarcualis; *M.O.* m. obliquus abdominis; *M.O.E.S.* m. obliquus abd. externus superficialis; *M.TR.* m. transversus abdominis; *M.R.A.* m. rectus abdominis.

lung, its medial fibres stretching forwards, ventral to the 4th and 5th vertebrae, to insert onto the lateral surfaces of the oesophagus (fig. 23) and the pericardium. Although they approach each other closely, the muscle is not, at this stage, associated with the m. rectus abdominis.

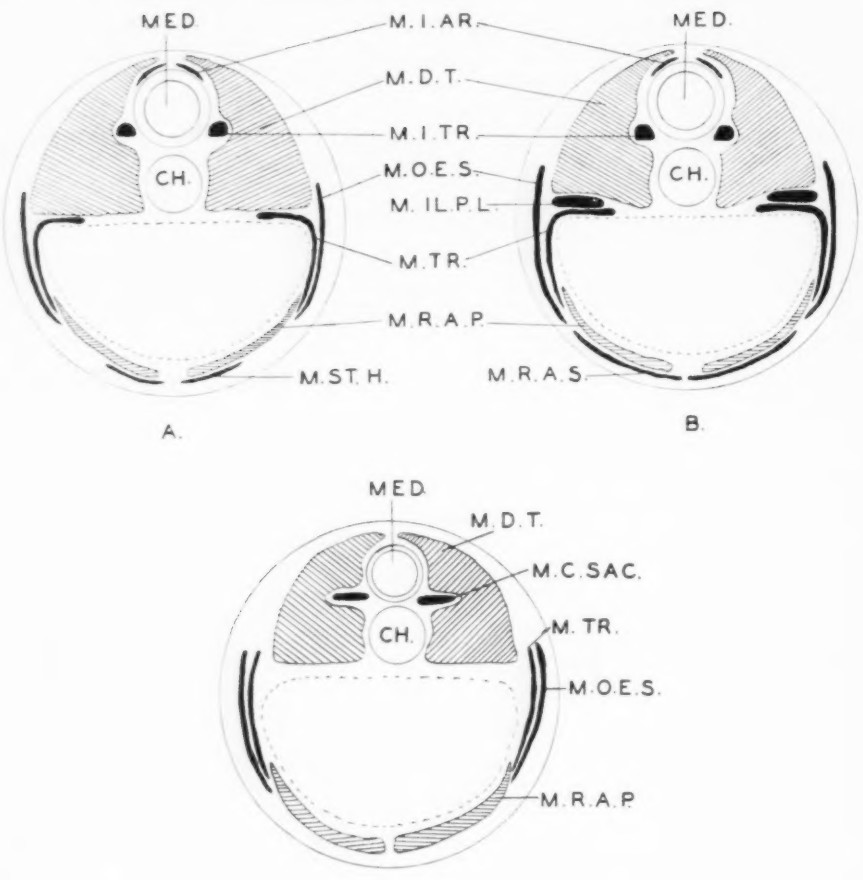

Fig. 28. Schematic diagrams of transverse sections through various regions of the trunk during metamorphosis. Secondary muscles in black, primary muscles oblique lines. A. The anterior region. B. The middle region. C. The posterior region. *MED.* medulla spinalis; *CH.* chorda dorsalis; *M.I.AR.* m. interarcualis; *M.D.T.* m. dorsalis trunci; *M.I.TR.* m. intertransversarius; *M.IL.P.M.* m. ileolumbalis, pars medialis; *M.IL.P.L.* m. ileolumbalis, pars lateralis; *M.O.E.S.* m. obliquus abdominis externus superficialis; *M.TR.* m. transversus abdominis; *M.R.A.P.* m. rectus abdominis profundus; *M.ST.H.* m. sternohyoideus; *M.R.A.S.* m. rectus abdominis superficialis; *M.C.SAC.* m. coccygeo-sacralis.

3. *Zonal muscles covering the trunk*

M. latissimus dorsi (figs. 22, 23 and 26)

This muscle of the shoulder girdle takes origin from an aponeurosis in front of the posterior attachments of the m. obliquus externus and m. transversus abd., and dorsally from the fascia dorsalis. It covers the outer surface of the m. obliquus abd. externus and overlaps a small portion of the m. pectoralis, pars

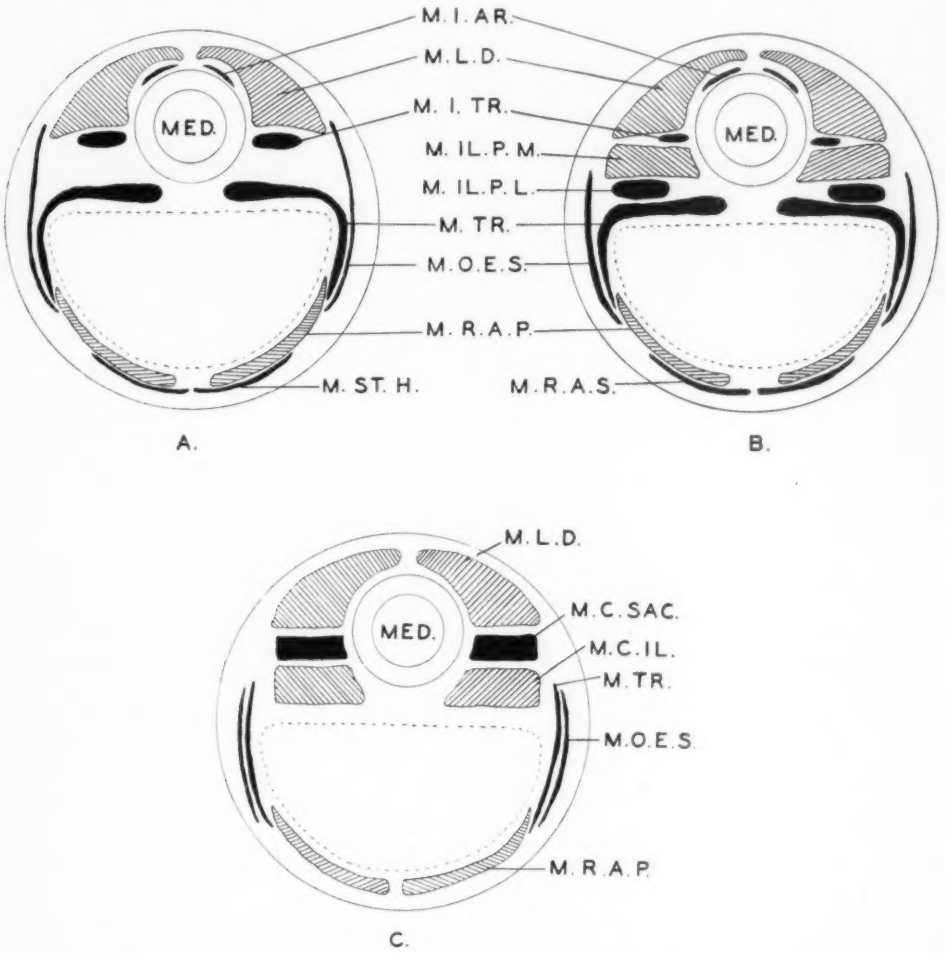

Fig. 29. Schematic diagrams of transverse sections through various regions of the trunk of a young post-metamorphic specimen. Secondary muscles in black, primary muscles oblique lines. A. The anterior region. B. The middle region. C. The posterior region. *M.I.AR.* m. interarcualis; *M.L.D.* m. longissimus dorsi; *M.I.TR.* m. intertransversarius; *M.IL.P.M.* m. ileolumbalis, pars medialis; *M.IL.P.L.* m. ileolumbalis, pars lateralis; *M.TR.* m. transversus abdominis; *M.O.E.S.* m. obliquus abdominis externus superficialis; *M.R.A.P.* m. rectus abdominis profundus; *M.ST.H.* m. sternohyoideus; *M.R.A.S.* m. rectus abdominis superficialis; *MED.* medulla spinalis; *M.C.SAC.* m. coccygeo-sacralis; *M.C.IL.* m. coccygeo-iliacus.

abdominalis. Anteriorly it shifts dorsally to cover the dorso-lateral surface of the suprascapula. The foremost fibres converge giving this muscle a triangular shape. It inserts onto the crista ventralis humeri.

M. pectoralis, pars abdominalis (figs. 22, 23 and 26)

This muscle takes origin from a posterior aponeurosis, and from an entirely new ventral fascia for the mm. pectorales. This fascia can easily be confused with the linea alba, but it has an entirely different origin. Posterior to the shoulder girdle it merges into the linea alba, with which it forms a folded vertical sheet of connective tissue which is sternogenic. Except for the medio-ventral portion of the m. rectus abdominis, it covers the ventro-lateral muscles of the trunk. It is slightly overlapped dorsally by the m. latissimus dorsi. Its anterior insertion reaches to the ventral surface of the crista ventralis of the humerus.

M. iliacus externus (figs. 22 and 26)

This massive muscle of the pelvic girdle takes origin from the ilial wing (fig. 26) by means of three distinct portions. Medially it is attached to the developing fascia lumbo-dorsalis which penetrates between the m. longissimus dorsi and the m. coccygeo-iliacus. Caudally it inserts onto the femur in the vicinity of the crista femoris.

These above-mentioned zonal muscles have developed very rapidly and become enormously extended during metamorphosis.

VOL 34 195

V. DISCUSSION

1. DEVELOPMENT OF THE SOMATIC MUSCLES IN GENERAL

The primary reason why mesoderm develops, is according to the English school, such as RAY LANKESTER, that of segregating reproductive from trophic endoderm. In the vertebrates the original gonadogenic function of the mesoderm is localized in the splanchnotome and confined to the genital ridge. Moreover the mesoderm has acquired other functions, such as blastogenesis, myogenesis, nephrogenesis and haematopoiesis. Skeletogenous and myogenic differentiations are intimately associated with each other and, during phylogeny, to a considerable extent affected each other. It is, therefore, surprising that phylogeneticists have chiefly paid attention to skeletal parts, in spite of the fact that the musculature also reflects phylogenetic relationships. Even from a study of fossilized skeletons fairly accurate conclusions can be drawn regarding the modifications of the muscles. The recognition of this fact was in a large measure responsible for the founding of the science of palaeobiology.

In many instances the modifications of the muscles are causal to the development of skeletal structures. It is, for example, evident that "the dorsal myotomes are causally responsible for a dorsal axial skeleton; it is only when the myotomes and, more particularly the medial muscle layer, grew downwards, that ventral skeletal parts, such as the appendicular, the zonal, the visceral and the sternal

skeleton reached any high grade of development" (DE VILLIERS, 1926, p. 67). Obviously the preservation of skeletons in the form of fossils gives this system priority in comparative anatomical research work, but conclusions arrived at from these data can often be denied, or qualified, when studying the ontogenesis of the musculature. It is also most probable that the muscular system possesses a high degree of phylogenetic plasticity, so that an investigation of its ontogenesis might provide a better understanding of the anatomy of fossils. It must, however, be stressed that such plasticity presents greater possibilities for larval reactions resulting in caenogenetic phenomena, which might conceal the real course of palingenesis.

The complete lack of literature concerning the ontogenesis of the musculature of specific amphibians makes a comparative discussion of my results almost impossible. Only a limited amount of work has been done on muscle embryology. Yet "embryological origin is here, as ever, an important criterion for identification of homologies" (ROMER, 1949, p. 254). It is, therefore, inevitable that any phylogenetic conclusions arrived at from the study of the development of the muscles of the trunk of *Xenopus laevis* will, to some extent, be speculative.

VOL.
34
1953

As stated in the introduction, each of the coelomic pouches is differentiated into a dorsal somite, composed of a sclero-myotome and dermatome, and a ventral part, the splanchnotome. The latter fulfils the primary function of the mesoderm in producing the gonads and forming the general non-metamerised coelome of vertebrates which is the result of the fusion of the consecutive splanchnocoels. The splanchnotome also gives rise to the visceral musculature. The somites retain the primary metameric arrangement, but in the adult this is confined to a few myomeres. The position of the myotomes is a convenient criterion for determining the identity of the individual metameres. Thus the vertebrae (originating from axial mesenchyme), myocommata and ribs are intermetamerically arranged. The arrangement of the vertebrae in the adult is a pseudo-metamerism.

In view of the publications of the 20th century it seems necessary to specify RABL's conception of mesenchyme. He obviously considered the sclerotome of *Amphioxus* to be the homologue of only the axial mesenchyme of vertebrates. The extension of the meaning of mesenchyme to include cells of non-mesodermal origin, and the interpretation that all the embryonic connective tissues represent mesenchyme, is mainly the invention of histologists. Comparative embryologists frequently use the term mesenchyme more in a histological than in a morphological sense. A single quotation from the histologist A. A. MAXIMOV will suffice to illustrate this statement: "The blood with its cellular elements, the blood vessels and the bloodforming organs, are also derivatives of the mesenchyme. The first endothelial cells are flattened mesenchymal cells joined by their edges to form a system of tubes" (1929, p. 146). This statement is not in agreement with the conclusively proved findings of ARNOLD LANG (1903) in his "Beiträge

zu einer Trophocöl-Theorie". A still more extended conception of mesenchyme is furnished by the embryologist SHUMWAY (1938): "The musculature of the vertebrate is derived from mesenchyme, of which the greater part originates from the myotomes and give rise to striated muscle cells ..." (p. 238).

As far back as 1907 VOIT directed the attention to the fact that recent interpretations of the term mesenchyme differ considerably from the conception of the brothers Hertwig. Research work revealed that cells which are histologically indistinguishable from the axial mesenchyme, take origin from the cutis, the splanchnotome, the ectoderm and even the endoderm. As a result of these facts VOIT came to the conclusion: "... dasz man nicht mehr wie bisher das Mesenchym als ein Derivat des mittleren Keimblattes und die aus dem Mesenchym entstehenden Organe als eine einheitliche Gruppe betrachten darf. Man musz vielmehr das Mesenchym heutzutage nur als einen histologischen Begriff auffassen." The histologists, embryologists and anatomists may accept this view, but for comparative anatomical and comparative embryological purposes. the axial mesenchyme, is of such morphological importance that it deserves special attention. Although sometimes indistinguishable from "other mesenchyme", it possesses a definite individuality in giving origin to specific structures. There definitely is an intermingling of axial and other mesenchyme cells (e.g. at the cutis-myocommata junctions), but it cannot be proved that the former has lost its identity. Probably the axial mesenchyme is only blastogenic and not myogenic. From a *histological* point of view my own observations show that mesenchyme cells (sensu latu) do participate in the construction of the secondary muscles, but that the origin of these cells remains a very contentious problem.

Although it is generally accepted that the myotome is the source of the somatic striated muscles, this view is denied by several authors, foremost of whom probably is LEWIS (1902). This author is followed by SCHMIDT (1925, 1927), KATZNELSON (1934, 1935, 1936) and others. The first two authors investigated the origin of the muscles of the extremities in mammals, whereas KATZNELSON interested himself in the muscles of the trunk in the urodele, *Salamandrella keyserlingi*. The latter author, being a histologist, came to the conclusion that part of the striated musculature of vertebrates is derived from the mesenchyme by means of local differentiation and without participation of the myotome.

It is impossible, when studying the differentiation of the mesenchyme, to distinguish histologically between the cells of different origin. The facts revealed by investigations can only be stated, but the migration routes of different mesenchyme cells cannot be traced to their full extent. In fact, RABL warned against interpretations based on incomplete observations: "Wenn man daher auch an mehr als einer Stelle die wünschenswerthe Klarheit vermissen wird, so kann ich doch den Vorwurf, den man mir daraus machen kann, nicht allzu schwer

VOL 34 195

nehmen; denn der Forscher soll die Wahrkeit über Alles halten; er darf sie nie der Klarheit zum Opfer bringen: denn was heute nicht ganz klar ist, kann es morgen werden; was aber heute eine Lüge ist, bleibt in alle Ewigkeit eine Lüge" (1889, p. 115).

KATZNELSON's observations on the histogenesis of the muscular tissue in *Urodela* induced him to conclude that the myotome is not the source of the secondary striated musculature. In contradicting the generally accepted view this author cited as evidence in chief the work of MAURER. He probably consulted only MAURER's contribution in O. HERTWIG's "Handbuch" (1906), and neglected to study his monographs on the development of the ventral somatic muscles of the trunk in *Urodela* and in *Anura*. Obviously it was not possible for KATZNELSON to gain a correct perspective of MAURER's investigations from the generalized description in the "Handbuch". MAURER himself was aware of "other" cells participating in the construction of these muscles, for, in 1895 he wrote: "Es scheint mir von grószter Bedeutung, dasz es hier sicher nachweisbar ist, wie zwischen dem ventralen Rand der Urwirbel-muskelmasse und dem dorsalen Rand des davon abgelösten ersten ventralen Muskelstreifens noch eiregelmäszig vertheilt abgelöste Zellenkomplexe in Bindegewebe sich befinden, die allmählich zur Muskelbildung herangezogen werden" (p. 235). It can readily be assumed that these cell complexes of MAURER are the same as the mesenchyme cells referred to by KATZNELSON. *Histologically* my own observations on *Xenopus* tally with the conclusions of KATZNELSON, where he maintains that part of the ventral musculature of the trunk is of mesenchymal origin. But I definitely cannot support his view that these mesenchymal muscles are in no way derived from the myotomes. My own observations clearly indicate that the secondary muscles develop by means of proliferations from the primary muscles. These liberated muscle cells are somehow changed into mesenchymatous cells which constitute the anlage of the myofibrillae. This is in accordance with MAURER's investigations where he states: "Jetz finden vielmehr Wucherungs- und Zerfallsvorgänge an den Elementen der primären Muskulatur statt, wodurch die ersten Muskelfasern allerdings zu Grunde gehen, zugleich aber das Material für die neu sich bildenden Muskelfasern liefern" (1895, p. 227). According to NISHI (1938) a similar statement was made by MÜLLER (1921) in a paper on the secondary muscles of the dorsal part of the trunk. This author regarded their formation as mainly due to a resorption and regeneration of muscle fibres. The rebuilding of new muscle fibres from the reduced primary muscles was also mentioned by DRÜNER (1904) (cited by LUBOSCH, 1938) and more recently, by GLÜCKSMANN (1934).

I can, however, confirm KATZNELSON's statements that there is no myoblast stage in the development of the secondary muscles, and that three stages can be distinguished in the formation of the fibres:

i) The stage of condensation and orientation of the "mesenchymal" nuclei;
ii) the stage of the appearance of myofibrillae, and
iii) the stage of the formation of muscular fibrils.

My observations also confirm KATZNELSON's statement, that the only histological difference between the development of the primary and secondary muscles is that the myofibrillae of the former develop from myoblast cells instead of from mesenchymatous cells. In his discussion of the secondary muscles of *Anura*, MAURER made a similar statement: "Es handelt sich nach meinen Befunden nicht einfach um Apposition von jungen Muskelfasern, welche sich aus embryonalen Muskelbildungszellen entwickeln, auf diese Weise entwickelt sich nur die primäre Muskulatur" (1895, p. 227). The only real difference between the primary and secondary muscles is, according to my own observations, the greater size of the muscle bundles of the former.

In 1902 ZIEGLER directed attention to the fact, that cells of myotomal origin can simulate mesenchyme cells; he states that: "... in den übrigen Segmenten lösen sie sich auf, und ihre Zellen sind von den umgebenden Mesenchymzellen nicht mehr zu unterscheiden" (p. 37). Undoubtedly KATZNELSON's conception of mesenchyme is a purely histological one, but his statement that the secondary muscles of the ventral part of the trunk do not, even in part, originate from the myotomes, cannot be accepted. He never mentions the probable or possible origin of the mesenchyme cells, yet he readily assumes that they are not derived from proliferations of the myotomes. A possibility that cannot be overlooked is that the mesenchyme cells participating in the formation of secondary muscles are intermediate cells, comparable with the osteoclasts of developing bone. I cannot imagine the process of the disintegration of muscle fibres without the aid of such amoeboid cells. I have not been able to demonstrate the actual transformation of myotome muscle fibres into mesenchyme-like cells from which new muscle fibres develop, but neither was KATZNELSON able to trace the origin of those mesenchyme cells. In a later paper (1936) KATZNELSON published the results of his investigations on the dorsal somatic musculature, his previous papers being mainly based on the development of the muscles of the abdominal wall. His material (*Salamandrella*) is the same microtomized series used for his previous investigations. At the dorso-medial aspect of the dorsal myotome he detected a projection of cells showing mitotic divisions, and which he termed the dorsal "Wachstumskegel". To this projection he ascribed the ability of forming new muscle fibres for the dorsal musculature. Judging from his illustration this "Wachstumskegel" apparently represents the proliferating part of the m. dorsalis trunci contributing towards the formation of the mm. interarcuales in *Xenopus*. The conclusion of KATZNELSON is that: "Bei Wirbeltieren findet in der postembryonalen (larvalen) Periode Neubildung von quergestreiften Muskelfasern statt. Als Quellen für diese Neubildung dienen die Reserven von

undifferenziertem Myoblastgewebe und das Mesenchym" (p. 388). This conclusion is more acceptable, but partly contradicts his previous statements. As he does not state which muscle is under discussion, it is difficult either to deny or qualify his findings.

According to my observations, the primary muscles develop from epithelium-like myoblast cells, whereas the secondary muscles are formed by means of proliferations from the former, in collaboration with mesenchymatous cells, which probably have a different origin. The possibility can, however, not be excluded, that undifferentiated myoblast cells also contribute to the formation of these muscles. It is clear that all the secondary muscles investigated by me develop in close association with the primary muscles. Not one of them exhibits an autochtonous origin from mesenchyme cells derived from sources other than the myotomes. To summarize the views of MAURER and KATZNELSON, it may be stated that, histologically, there are no fundamental differences between their findings. The latter author regards MAURER's cell complexes and other pre-muscular cells of myotomal origin as mesenchyme. KATZNELSON denies, that they originate from the myotome, but gives no convincing proof of his argument.

OL.
34
953

According to GLÜCKSMANN (1934) the dermatome participates in forming myoblast cells from which the primary muscle fibres are developed. Owing to the vast amount of yolk it was impossible to determine this with certainty in *Xenopus*. MAURER (1892) never denied such a possibility when commenting on similar remarks by previous authors, but merely stated that he could not observe a participation of the dermatome in forming myoblast cells. It must, however, be borne in mind that genuine dermal muscles, such as the tunica dartos of mammals and certain nasal muscles of reptiles are derived from the cutis. These dermal muscles are not to be confused with the facial muscles, which are of visceral origin.

2. DEVELOPMENTAL AND ADULT CONDITIONS OF SPECIFIC MUSCLES

a. *General topography*

During ontogeny the musculature of the trunk differentiates into distinct dorsal and ventral parts, the latter developing from the projection of the myotome ("Urwirbelfortsatz"). The muscles generally are also divided into dorsal epaxial (epaxonic) and ventral hypaxial (hypaxonic) parts, the partititon between them being a horizontal myoseptum of axial mesenchymous origin. STANNIUS (1856) introduced the terms hypaxonic and epaxonic, but RABL (1893) was the first to define them exactly. Owing to the fragmentary remnants or perhaps total absence of this horizontal connective tissue plate in the *Anura* this distinction is of very little morphological significance. These two divisions do not correspond with the primary myotome and "Urwirbelfortsatz" respectively, for the horizontal myoseptum cuts the dorsal myotome at the approximate level

of the transverse processes of the vertebrae. The only real criterion for recognizing ep- and hypaxial muscles is their innervation, the latter being innervated by the ventral branch of the ventral root of the spinal nerve and the former by the dorsal branch. For comparative anatomical purposes this constancy of muscular nerve supply, elaborated in great detail by FÜRBRINGER, is of major importance. Irrespective of several striking exceptions, innervation can be used as the chief guide in the establishment of muscle homologies, especially within a single class (HAINES, 1935, LUBOSCH, 1938). The primary somatic musculature of vertebrates (with the exception of the cyclostomes) is thus partitioned into ep- and hypaxial muscles by a horizontal myoseptum, and into myomeres by means of the myocommata. Where remnants of the latter can be traced in more highly developed muscles they are known as inscriptiones tendineae (VERSLUŸS, 1924).

The anterior part of the somatic hypaxonic muscles is also naturally divided into epi- and hypobranchial portions, a division caused by the presence of gill slits in the larval or adult stages. A dorsal bundle of the hypaxial muscles joins the epibranchial portion in the primary condition. Apart from these topographical divisions the muscles of the trunk can also be classified according to the ontogenetic period during which they develop. In his monograph on *Urodela* MAURER (1893) distinguished between the primary and secondary muscles, the latter developing during or immediately before metamorphosis. The primary or autochtonous muscles (VERSLUŸS, 1924) develop from the somite with its ventral projection, the "Urwirbelfortsatz", during the early stages of ontogeny. According to MAURER (1893) the secondary muscles, covering the ventral and lateral parts of the abdominal wall (i.e. those originating from the "Urwirbelfortsatz"), do not predominate in the majority of *Urodela*. Only the more terrestrial caducibranchiates exhibit better developed secondary muscles in the adult stage. In this amphibian order the primary muscles are represented by the m. dorsalis trunci, m. rectus abdominis profundus, and the m. rectus lateralis. Shortly before metamorphosis commences the secondary muscles, including the m. rectus abdominis superficialis, m. transversus, m. obliquus externus superficialis and m. subvertebralis, develop from the primary group.

In *Anura* conditions differ from those in *Urodela* in a few important respects. In the former the secondary muscles of the abdominal wall are reduced to the m. transversus abdominis and m. obliquus abd. externus superficialis, whereas the primary group is represented by a single m. rectus abdominis. In contrast to the majority of urodeles the secondary muscles predominate in the covering of the abdominal cavity. In connection with the vertebral column the dorsal musculature exhibits a differentiation into short muscles. A very important difference, according to MAURER (1895), is the late development of the m. obliquus abd. externus in *Anura*. I shall later explain that I cannot endorse this view. In a list of the primary somatic muscles retained in the adult anuran

VOL. 34 1953

trunk the following must be mentioned: m. longissimus dorsi, m. ileolumbalis, pars medialis, m. coccygeo-iliacus, m. rectus abdominis. The secondary muscles are represented by the mm. interarcuales, mm. intertransversarii, m. transversus abdominis, m. obliquus abdominis externus superficialis, m. sternohyoideus and, perhaps, the m. rectus abdominis superficialis (figs. 27, 28 and 29).

When reviewing the conditions of the somatic musculature of the trunk obtaining in the young adult (early post-metamorphosis specimen) of *Xenopus*, and comparing them with the muscles of the old adult, as described by GROBBELAAR (1924), it becomes evident that the whole picture changes in the direction of a more compact covering of the trunk. There is a strong tendency for muscles which were intimately associated with one another to become completely fused. Separation by means of dissection is thus rendered impossible. To check the conclusions of GROBBELAAR, I dissected several old specimens of *Xenopus*, but could find no differences from the data in his excellent monograph. The muscles of the young post-metamorphic *Xenopus* bear a very strong resemblance to those of the adult *Rana* as described by GAUPP in the "Anatomie des Froches" (1896). The only real difference is the greater relative area occupied by the zonal muscles covering the trunk. The adult *Xenopus* can therefore be considered *as a very specialized amphibian!* These specializations may be due either to neoteny or to adaptations to a permanent aquatic life.

When dealing with each muscle separately, I shall constantly be comparing young and old adult stages of *Xenopus* with each other and discuss the comparative implications.

b. *Muscles originating from the m. dorsalis trunci* (VERSLUŸS)

The m. dorsalis trunci flanking the vertebral column, is the primary undifferentiated dorsal muscle mass of fishes and urodeles. In *Anura* this muscle gives origin to the "short" secondary muscles of the vertebral column as well as to separated portions underlying the transverse processes. The remaining dorsal layers of the m. dorsalis trunci in *Anura* constitute the

M. longissimus dorsi

In the adult *Xenopus* this muscle exhibits approximately the same extension and attachments as in the young post-metamorphic specimen. The fascia dorsalis on its dorsal and lateral sides and the ligamentum intermusculare dorsally separating the left and right mm. longissimi, are well-developed. The most medial fibres of this muscle are now very intimately associated with all the mm. interarcuales and mm. intertransversarii "so dasz nur eine künstliche Trennung möglich ist". (GROBBELAAR, 1924.)

Compared with other *Anura* the m. longissimus dorsi of the young post-metamorphic specimen of *Xenopus* resembles that of the adult of *Breviceps*

(BEDDARD, 1908) in taking origin from approximately the posterior extremity of the urostyle. In the adult *Xenopus* it arises from the anterior two-thirds (GROBBELAAR), in *Bufo* from the anterior half (BIGALKE) and in *Rana* from the anterior third (GAUPP) of the urostyle. There is moreover no constancy in the number of remaining inscriptions between its myomeres in different *Anura* : *Bufo* having seven, *Xenopus* eight and *Rana* nine.

M. ileolumbalis (HOFFMANN)

This muscle, as described by GAUPP for *Rana*, consists of a medial and lateral portion, both of which, according to my own observations on *Xenopus*, must be considered as separate muscles. GAUPP found indications that the pars lateralis and the pars medialis being of different origins, but he could not determine this with certainty. He states: "Der Ileolumbaris ist ein ausserordentlich interessanter Muskel insofern, als in ihm wahrscheinlich dreierlei verschiedene Elemente vereinigt sind. Es scheinen nämlich die medialen Partien hervorgegangen aus den dorsalen, die ventralen und segmentirten lateralen aus den ventralen Segmenten des Stammesmuskels der Larve, während die unsegmentirten, an der Kante gelegenen und zum Becken gehenden als Becken-(Extremitäten-) Muskel aufzufassen sind" (1896, p. 113). On this GROBBELAAR (1924) commented by stating that the single m. ileolumbalis "bei *Xenopus* und *Pipa* dieser unsegmentierten, zum Becken gehenden Partie des m. ileolumbaris bei *Rana* entspricht". The ontogeny of *Xenopus*, however, proves the conclusion of both GAUPP and GROBBELAAR to be incorrect. The m. ileolumbalis of the adult *Xenopus* represents the product of fusion of the pars medialis and lateralis. In the young post-metamorphic specimen the p. medialis takes origin both from the anterior border of the transverse process of the sacral vertebra and from the medial surface of the tip of the ilial wing, whereas the pars lateralis arises from the lateral surface of the latter skeletal structure. These attachments, as well as the total separation from each other of the two portions resemble a condition obtaining in the adult *Bufo* (BIGALKE, 1926). In *Rana* the two portions are separated in their caudal sections only (GAUPP, 1896). The origin of the m. ileolumbalis from the entire tip of the ilial wing in the adult *Xenopus*, confirms the contention that it represents a fused pars lateralis and medialis. Judging from BEDDARD's description (1906), approximately similar conditions obtain in *Breviceps*.

Concerning the ontogenesis of these muscles, the conditions in *Xenopus* reveal that the pars medialis is a separated ventral portion of the m. dorsalis trunci, whereas the pars lateralis originates from proliferations of the ventro-lateral part of the m.d. trunci, in collaboration with mesenchyme-like cells. The ventral musculature does not contribute towards the formation of these muscles, as GAUPP maintained. The two portions also differ in respect to their mode of

VOL. 34 1953

origin: the pars medialis being a primary and the p. lateralis a secondary muscle.

As regards the separation of the pars medialis from the m. longissimus dorsi—a process which was still in progress during the early post-metamorphic stage—the adult *Xenopus* shows a horizontal connective tissue plate separating them. This plate partly develops from connective tissue cells of the fascia dorsalis, spreading in a medial direction at the level of the ribs and transverse processes of the vertebrae. At intervals the remnants of myocommata join this tissue, thus constituting the partitioning wall called the fascia lumbodorsalis (see horizontal myoseptum).

M. coccygeo-iliacus and m. coccygeo-sacralis

In the adult *Xenopus* these two muscles are inseparable, and GROBBELAAR only recognized one massive m. coccygeo-iliacus. According to NISHI (1938) *Xenopus* and *Pipa* are the only members of the *Anura* which apparently lack a m. coccygeo-sacralis. Judging from the relations during the metamorphosis of *Xenopus*, the coccygeo-iliacus of *Pipa* probably also represents a fusion of the latter muscle with the m. coccygeo-sacralis. As in the m. ileolumbalis, the coccygeal muscle of *Xenopus* is a composite muscle arising from the fusion of a primary (postero-ventral part of the m. dorsalis trunci) and a secondary muscle, represented by the m. coccygeo-sacralis. According to HOFFMANN (1873) the absence of a separate m. coccygeo-sacralis is due to the fusion of the sacral vertebra with the urostyle.

The young post-metamorphic specimen of *Xenopus* shows topographic positions and attachments of both the iliacal and sacral coccygeal muscles similar to those of *Rana* and *Bufo*. A point of difference is the insertion of medial fibres of the m. coccygeo-sacralis onto the neural arch of the sacral vertebra in *Rana* (GAUPP, 1896). GAUPP interpreted these fibres as representing the hindmost m. interarcualis. In *Xenopus* there are no attachments to the neural arch, and the whole m. coccygeo-sacralis apparently represents the most posteriorly situated m. intertransversarius. The ontogenetic evidence, concerning this matter, of the manner, place and time of development, supports this conclusion. GAUPP maintains that only the lateral part of the m. coccygeo-sacralis corresponds to the mm. intertransversarii. During the metamorphosis of *Xenopus* an independent m. interarcualis develops between the sacral vertebra and the posterior part of the urostyle. Such fibres become completely fused with the overlying m. longissimus dorsi during later stages. This is sufficient evidence that, in *Xenopus* at least, the last m. interarcualis is not incorporated in the m. coccygeo-sacralis. The fusion in *Rana* of the fibres of this m. interarcualis with the muscle in question, is possible, but highly improbable.

The m. coccygeo-iliacus is separated from the m. dorsalis trunci in approximately the same manner as the m. ileolumbalis, pars medialis, i.e. by means of

penetrating connective tissue interconnecting the remnants of the myocommata. This connective tissue plate (fascia lumbodorsalis) is also regarded as part of the fascia dorsalis. The m. coccygeo-iliacus constitutes the posterior continuation of the m. ileolumbalis, pars medialis, and both represent the ventral part of the original m. dorsalis trunci.

Mm. intertransversarii

In the adult *Xenopus* these muscles all join the m. longissimus dorsi, but the insertions of the m. intertransversarius capitis superior and inferior on the dorsal and ventral aspect of the skull respectively, are still indicated (GROBBELAAR, 1924). The lateral m. intertransversarius, extending between the distal ends of the 2nd and 3rd ribs in the early post-metamorphic stage, cannot be traced in the adult and probably also fuses with the m. longissimus dorsi. This m. intertransversarius is retained in the adult stage of *Rana* (GAUPP) and *Bufo* (BIGALKE). In most of the *Anura* that have been investigated the mm. intertransversarii behind the 4th vertebra are intimately associated with the m. ileolumbalis, whereas they join the ventral part of the m. longissimus dorsi in *Xenopus*, but this does not represent a major deviation. The mm. intertransversarii, being secondary muscles, develop from the middle of the medial surface of the m. dorsalis trunci, opposite the transverse processes of the vertebrae. In fact, they partly develop in (not from) the connective tissue which, during a later stage, will form part of the partitioning wall between the m. logissimus dorsi and the m. ileolumbalis. These intervertebral muscles are situated in an intermediate position between the m. longissimus dorsi and the future m. ileolumbalis, pars medialis. Judging from its innervation the former muscle is epaxial and the latter hypaxial, whereas the mm. intertransversarii are supplied by either or both the dorsal and ventral branches of the ventral roots of the spinal nerves (GAUPP, 1896). It is, therefore, evident that they can readily join either the dorsal or the ventral part of the original m. dorsalis trunci. The fact that they actually join the m. longissimus dorsi in *Xenopus* may be of taxonomic, but not of morphological significance. As previously stated, the m. coccygeo-sacralis represents the hindmost m. intertransversarius.

Mm. interarcuales (Nishi)

When comparing a young post-metamorphic specimen of *Xenopus* with the older adult, the striking feature once more is the intimate association between secondary (mm. interarcuales) and primary (m. longissimus dorsi) muscles; this is achieved during the latest stages. In both *Rana* and *Bufo* the mm. interarcuales behind the 4th vertebra are independent of the m. longissimus dorsi although, anteriorly, they are likewise represented by the deepest layers of this muscle.

VOL. 34 1953

M. subvertebralis

It is generally accepted that a m. subvertebralis is absent in *Anura* (CORDS, 1923). My own investigations supports this view.

Horizontal myoseptum

In fishes this horizontal connective tissue plate is a conspicuous partition between the epaxial and hypaxial somatic muscles. Its alleged presence and its homologies in the *Tetrapoda* is a much debated question among comparative anatomists. EMELJANOV (1933) maintains that, apart from a rudimentary septum in *Urodela*, a horizontal myoseptum is absent in the *Tetrapoda*. MARCUS (1937), however, following up this statement of EMELJANOV, demonstrated the presence of a horizontal myoseptum in the *Gymnophiona*. During the ontogeny of *Xenopus* no indications could be detected of any structures, which could be homologized with this septum in fishes. According to MARCUS the septum develops during early ontogeny and in very much the same manner as does the myocomma. An intermuscular fissure also preceeds the migration of mesenchyme cells constituting this horizontal connective tissue plate. These processes cannot be demonstrated for *Xenopus*. I am rather inclined to accept the view of VERSLUŸS: "Bij de Tetrapoden wordt door de oplossing der zijderompspier in taljijke selfstandige spierindividuën het horisontale myoseptum minder duidelik; de dwarsuitsteeksels der werwels en een daarvan uitgaande peesplaat, de fascia lumbodorsalis, geven echter nog zijn ligging aan en de scheiding in dorsale en ventrale rompspieren blijft bestaan" (1924, p. 406).

The fascia lumbodorsalis, in fact, forms part of the fascia dorsalis in the same way as does the fascia intermuscularis between the dorso-medial portions of the two mm. longissimus dorsi. In the adult anuran the fascia lumbodorsalis can be distinguished as the partitioning connective tissue separating the m. longissimus dorsi from its derivatives, the m. ileolumbalis, pars medialis anteriorly and the m. coccygeo-iliacus posteriorly.

It is generally accepted that the anlagen of the dorsal ribs are situated where horizontal myoseptum cuts the myocommata. My co-worker, Mr. SMIT, who investigated the development of the ribs from the same sections, could not find any trace of a true horizontal myoseptum. The fascia lumbodorsalis of the adult *Xenopus* cannot, therefore, be regarded as a true horizontal myoseptum since it develops very late during the metamorphosis. It represents a structure of anatomical, but not of morphological significance. As VERSLUŸS maintains, it only serves for attachment of muscles and, topographically, indicates the primary position of the true horizontal myoseptum. The muscles dorsal to the fascia lumbodorsalis (epaxial muscles) are typically innervated by dorsal branches, and those underlying it (hypaxial muscles) by ventral branches of the ventral roots of the spinal nerves.

c. *Muscles originating from the "Urwirbelfortsatz"*

The primary ventral projection of the somite ("Urwirbelfortsatz") contains the elements of all the muscles covering the ventral, lateral and even part of the dorsal aspect of the abdominal cavity.

M. rectus abdominis

During metamorphosis it becomes evident that this muscle represents a fusion of the m. rectus abdominis profundus and m.r.a. superficialis in the old adult. The only part of this muscle still distinguishable as superficialis in the old adult is a ventro-medial portion inserting onto the dorsal surface of the sternum. Antero-dorsally the m. rectus abdominis joins the longitudinal fibres of the m. transversus abd. in covering the pericardium of the heart.

Nowhere in the available literature I could find any reference to the presence of a rectus abdominis superficialis in *Anura*. Before commencing my investigations, however, Prof. DE VILLIERS pointed out to me that he had seen a superficialis in young post-metamorphic specimens of *Xenopus*. The only other reference to the possible persistence of a m.r.abd. superficialis in an adult frog concerns the superficial fibres in *Bombina* observed by MAURER (1895). In view of the primitiveness of *Bombina*, this may well be the superficial part of the m. rectus abdominis. I could not find any traces of a m. rectus abd. superficialis either in the larval or adult stages of *Ascaphus*. The conditions obtaining in *Xenopus* confirm MAURER'S opinion that the m. rectus abdominis of *Anura* represents the elements of both the profundus and superficialis.

The m. rectus abdominis of *Xenopus* differs from that of *Rana* and *Bufo* in respect of its posterior portion. The above description of the young post-metamorphic specimen makes it clear, that this is due to the development of the epipubis. This structure develops as a chondrification of the linea alba in the midventral line (DE VILLIERS, 1925) and separates the posterior projections of the two rectus muscles from each other. Since the epipubis develops autochthonously in front of the pelvis, the m. rectus abd. attaches itself to its dorso-lateral surface in stead of to the front margin of the pelvis as is the case in *Rana* and *Bufo*. While studying the development of the epipubis in *Xenopus*, DE VILLIERS (1925) noticed the occurence of an epipubic muscle inserting onto its dorsal surface. He was of opinion that this muscle (m. epipubicus—GROBBELAAR) secondarily acquired relations with the epipubis. My own observations of earlier stages confirms this assertion, but the m. epipubis does not originate from the rectus abdominis in the form of a muscle of the trunk. On the contrary, it develops from the mass of myogenic tissue of the pelvic girdle. There is, however, no proof that the muscles of the pelvic girdle do not, at least partly, originate from the m. rectus abdominis (fig. 30). In fact, during the formation of the anlage of the hind limb-bud the m. rectus abd. constantly proliferates

VOL.
34
1953

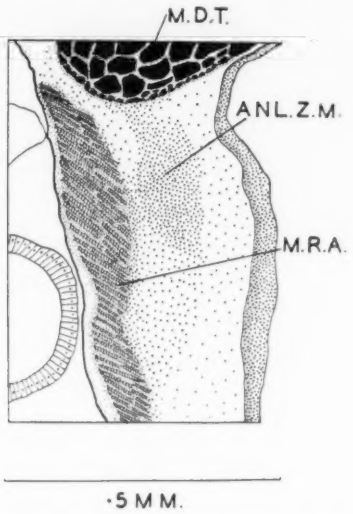

Fig. 30. Transverse section through the postero-lateral part of the trunk to show the proliferations of the m. rectus abdominis and the anlage of the pelvic muscles. Stage 54. *M.D.T.* m. dorsalis trunci; *ANL.Z.M.* anlage of the zonal muscles; *M.R.A.* m. rectus abdominis.

cells which migrate in the direction of the former. This problem, however, needs further investigation. A cursory inspection of the available material of *Ascaphus* seems to support this impression. During subsequent stages in *Xenopus* the m. epipubis shifts forwards, attaching itself to the antero-dorsal surface of the epipubis.

The origin of the muscles, somatic as well as visceral, surrounding the anal region, including the persistence of a m. lateralis in the larval stages, needs further investigation.

M. sternohyoideus

In the adult *Xenopus* this secondary muscle very intimately associates itself with the rectus abdominis. GROBBELAAR (1924) found it a very poorly developed muscle. Its inconspicuousness in the adult—in contrast to conditions obtaining in the early post-metamorphic stage—is due to its intimate relation with the m. rectus abd. This intimacy mainly affects the lateral portion (pars lateralis of *Rana* and *Bufo*) of the m. sternohyoideus, the pars medialis being the only distinguishable part. As revealed by its development the m. sternohyoideus is formed by means of the fusion of two muscle derivatives of the m. rectus abdominis, corresponding to the pars lateralis and pars medialis of *Rana* and *Bufo*. As maintained by GOETTE (1875) there is no doubt, that the m. sternohyoideus is a derivative of the m. rectus abdominis exclusively. According to NOBLE (1931) the m. sternohyoideus "is part of the hypaxial system, but its

union with the rectus is apparently secondary, since the labyrinthodonts had a better developed pectoral girdle than modern urodeles, and this would have separated the two muscles (MILNER, 1925). The condition in *Salientia* where the muscles are separate, although sometimes overlapping, is more primitive" (p. 254). In the light of the ontogenetic data obtained from *Xenopus*, this deduction by NOBLE seems highly probable.

M. obliquus abdominis

According to MAURER (1895) the dorsal part of the "Urwirbelfortsatz", i.e. the subsequent primary ventral musculature, represents the m. obliquus abd. internus only. Ontogenetic evidence derived from a study of *Xenopus*, however, indicates that the elements of the m. obliquus abd. externus are also incorporated in this anlage. It is clear that this muscle (m. obliquus abd.), during later stages of ontogeny, gives origin to the m. obliquus abd. externus superficialis by means of delamination (fig. 6). On its medial side the m. obliquus abd. externus superficialis and m. transversus abd., should thus represent the m. obliquus abd. externus profundus and m. obliquus abd. internus. These two muscles are primary muscles, disappearing during the subsequent stages of metamorphosis. Their fibrils are probably transformed into muscle building cells which participate in the formation of the superficial external obliquus and transversus muscles.

VOL. 34 1953

After comparing the conditions obtaining in *Urodela* and *Anura*, MAURER maintained that the inner muscle layer of the adult anuran, must be the m. transversus abd., it being a secondary muscle. Although several authors after MAURER still regarded this muscle as the m. obliquus abd. internus, its mutual relations to other muscles during ontogeny, and its topography in adult specimens, proves MAURER's conclusion to be correct.

As regards the m. obliquus abd. externus MAURER maintained that its first appearance during ontogeny synchronizes with the anlage of the m. transversus abd. But, he also assumed that the former muscle represents only the m. obliquus abd. externus superficialis. This, also when compared with the urodeles, is a secondary muscle. My own investigations corroborate MAURER's findings, and the outer layer of the abdominal wall of the adult anuran must therefore be considered homologous with the m. obliquus abd. externus superficialis of *Urodela*. In fact, my interpretation of the dorsal part of the "Urwirbelfortsatz" makes this assumption more acceptable. The causative circumstances (ontogenetic or phylogenetic) which led to the alleged late appearance of the m. obliquus abd. externus during ontogeny, evidently presented MAURER with a major problem. He could find no answer to this question and probably attributed it to caenogenetic alterations. I am rather inclined to believe that the dorsal part of the "Urwirbelfortsatz" of *Anura* represents both the m. obliquus abd. externus and internus as it does in *Urodela*. In the latter group these two

muscles are distinctly separated during the early stages of development, but this condition need not necessarily be primitive, the *Urodela* being a notorious group. The *Anura* as a group, are inclined towards reduction of the muscles of the trunk. These conclusions are not speculative: the evidence obtained from the manner in which the m. obliquus abd. externus superficialis develops is highly convincing. It arises as a delamination of the m. obliquus abd., but its morphology can only be established with the aid of a very complete series. The transformation of muscle fibres into pre-muscular cells probably is a very rapid process, a fact which may have been responsible for MAURER's inability to observe the real development of the m. obliquus abd. externus superficialis. According to him this muscle develops as follows: "Dieser Muskel kann nur aus bis zu seiner Bildung indifferent gebliebenen Muskelbildungszellen entstehen, welche entweder ebenfalls bei dem Herabwachsen des ventralen Myotomfortsatzes hier zunächst indifferent blieben, oder aber vom ventralen Ende dieses Fortsatzes aus längs dessen lateraler Fläche in die Höhe rückten und dann in einer bestimmten Entwicklungsperiode sich zu Muskelfasern heranbildeten. Ich neige dieser letzten Auffassung zu,..." (1895, p. 239). This statement suggests that a secondary muscle has a myoblastic origin. As previously mentioned, this cannot be demonstrated, but we can readily accept that other "indifferent gebliebene Muskelbildungszellen" of unknown origin participate in the formation of the superficial m. obliquus abd. externus.

Briefly the development of the ventral musculature of the trunk of *Xenopus* proceeds as follows: As in *Urodela*, the "Urwirbelfortsatz" contains the elements of both the m. rectus abdominis (ventrally) and the m. obliquus abd. internus and externus (dorsally). Shortly before metamorphosis the undifferentiated m. obliquus abd. gives rise to a medial m. transversus abd. and a lateral m. obliquus abd. externus superficialis. There is no ontogenetic connection between these two secondary muscles and the dorsal myotome. The remaining parts of the m. obliquus abd. (obliquus abd. internus + externus profundus) disappear during subsequent stages, its transformed fibres probably still contributing to the formation of the previously mentioned secondary muscles. During metamorphosis the ventral part (m. rectus abdominis) of the "Urwirbelfortsatz" gives origin to the m. sternohyoideus and m. rectus abdominis superficialis in a similar manner (figs. 27, 28 and 29).

M. obliquus abdominis externus superficialis

A comparison of the early post-metamorphic specimen with the adult shows this muscle to be less extensive in the latter. Anteriorly the pars scapularis probably fuses with the zonal muscles, its anterior insertion now being on the coracoid and in association with the m. transversus abd. and m. rectus abdominis. Posteriorly the enormously developed m. latissimus dorsi and m. pectoralis, pars abdominalis replace the larval attachment of the superficialis and the latter

then becomes attached to the aponeuroses of these zonal muscles. The m. latissimus dorsi is probably the causative factor in the non-development of the m. cutaneus abdominis in *Xenopus*. During the early stages of metamorphosis the m. obliquus abd. externus superficialis is a bulky muscle in comparison with the poorly developed m. transversus abd. During the later stages, however, these conditions are reversed, and the m. transversus abd. develops into an extensive muscle in the adult. According to HOFBAUER (1933) similar conditions obtain in the permanently aquatic *Urodela* where the m. transversus is relatively larger. This adaption to an aquatic life probably also applies to *Xenopus* and *Pipa* (BEDDARD, 1895). Adults of both *Rana* and *Bufo* possess a separate pars scapularis of the m. obliquus abd. externus.

M. transversus

In the adult *Xenopus* this muscle is associated with the m. rectus abdominis and m. obliquus abd. externus in the vicinity of the heart. Its dorsal fibres, running from the ilium to the oesophagus, over dorso-lateral surfaces of the lungs, are probably homologous with Beddard's "pulmo-oesophageal muscle" in *Pipa* and *Xenopus*. As in *Rana* and *Bufo*, a pars iliaca, pars dorsalis and pars vertebralis can be distinguished, the latter extending to the lateral and dorsal surfaces of the pericardium.

The fibres of the m. transversus are directed postero-ventrally, and those of the m. obliquus externus superficialis run in the opposite direction.

d. *Zonal muscles of the trunk*

The large area occupied by the m. latissimus dorsi and by the m. pectoralis, pars abdominalis in the adult *Xenopus* and *Pipa*, where similar conditions obtain, was commented upon by FÜRBRINGER (1874), MAURER (1895), BEDDARD (1896) and GROBBELAAR (1924). MAURER's explanation of the possible reason for their extensive development, is quite plausible. He holds that it is an adaptation to aquatic life, because these muscles assist the well-developed hind legs used in swimming. These muscles attach themselves to the anterior margins of the muscles of the hind limb, effecting a tensile force on the shoulder girdle, thus assisting in the swimming movement. The same author further compared *Xenopus* with *Ceratophrys* which, although possessing poorly developed forelimbs has a small m. latissimus dorsi and m.p., pars abdominalis. *Xenopus* and *Ceratophrys* thus represent the two extremes with *Rana* in an intermediate position. In this respect GROBBELAAR (1924) comments on the m. latissimus dorsi as follows: "Bemerkungswert ist die verschieden weite Ausdehnung dieses Muskels. Bei Xenopus erstreckt er sich auf die ganze Rückengegend, bei Pipa nur auf den hintersten, bei Opisthoglossen dagegen auf den vordersten Teil. In dieser Beziehung weisen Pipa und die Opisthoglossen die beiden Endpunkte zweier

ganz verschiedener Entwicklungsreihen auf, deren Angänge mit Hilfe des vermittelnden Glieden von Xenopus in ähnlichen Bildungen zu suchen sind, wie sie bei den Urodelen noch jetz existieren. Pipa zeigt in seinem Ursprunge die einseitigste Entwicklung" (p. 137).

The m. iliacus externus forms the major part of the posterior portion of the musculature of the trunk in *Xenopus*. There is, however, no major deviation from conditions obtaining in other *Anura*.

As regards the origin of the zonal muscles, it can readily be assumed, as BRAUS (1907), GOODRICH (1930) and VAN PLETZEN (in press) maintain, that they are derivatives of the myotome. The possibility that the pelvic muscles may arise partially from proliferations of the m. rectus abdominis merits investigation.

OL.
34
953

3. ADAPTATIONS AND AFFINITIES OF *XENOPUS*

In NOBLE's recent classification of the *Anura* (1931), *Xenopus* is classified under the *Pipidae*. The African pipids differ strikingly from the South American genera both in appearance and in life history, and they may, according to NOBLE, conveniently be placed in different subfamilies. The *Pipidae* thus comprises the *Xenopinae*, including *Xenopus, Hymenochirus* and *Pseudhymenochirus* and the *Pipinae* which includes *Pipa, Protopipa* and *Hemipipa*. These aglossal frogs are purely aquatic, having lost a tongue and movable eyelids (except *Pseudhymenochirus* which retains lower eyelids) in correlation with his habitat (NOBLE, 1931). It is generally accepted that the *Pipidae* are a primitive anuran family, probably only exceeded in primitiveness by the *Leiopelmidae* and *Discoglossidae*. As regards the musculature I fully subscribe to the following view of VAN PLETZEN (in press) who studied the ontogenesis and morphogenesis of the breast-shoulder apparatus of *Xenopus:* "It cannot be pretended that a study of the ontogenesis and adult anatomy of the breast-shoulder apparatus of a single genus can be conclusive of the conditions obtaining in the *Pipidae* as a whole. Since this family is admittedly neotenic, detailed comparison with the primitive *Anura* such as the *Leiopelmidae* and the *Discoglossidae* is dangerous, and utmost care should be exercised not to homologise neotenic features of the former family with actually primitive features of the latter two families."

Comparative anatomical investigations of the musculature of *Xenopus* were carried out by earlier workers such as FÜRBRINGER, MAURER and BEDDARD and, more recently by NOBLE (1922), GROBBELAAR (1924) and MILLARD (1949). Their conclusions are based exclusively on adult anatomical data. But ontogenetic data of all the pipid genera and of the *Leiopelmidae* and *Discoglossidae* should be compiled to estimate the exact interrelationships of these three anuran families (VAN PLETZEN, in press). For detailed discussion of possible pri-

mitive and specialized features, other than those of the musculature of the trunk, the reader is referred to MILLARD (1949).

Before reviewing the phylogenetic evidence obtained from the ontogeny of the somatic muscles of the trunk, I shall discuss the general statements and conclusions arrived at by MILLARD in the above-mentioned paper. She maintains that: "The *Pipidae* are, however, not only primitive and neotenic, but possess many characteristic of a specialized nature." Apparently she regards neoteny as being in the same category as primitiveness and contrasts it with specializations. The historical background, meaning and importance of the term, and phenomenon of neoteny, will be discussed in a future paper. Suffice it to state that although the term was introduced by KOLLMANN in 1883, the significance of this phenomenon for comparative anatomy and phylogeny was first realized and elaborated by VERSLUŸS (1909, 1923, 1924, and 1931). Three types of neoteny can be distinguished namely: 1. partial neoteny (designated by KOLLMANN for the hibernation of tadpoles), 2. total neoteny (arresting of the development of the whole animal at a certain stage e.g. the axolotl) and 3. neotenic features (VERSLUŸS) or organ neoteny (DE VILLIERS) i.e. neoteny affecting only certain systems or organs. These larval features persisting in the adult (organ neoteny) must be features which had been further developed (seemingly more specialized) in their ancestors, otherwise they would represent primitive conditions. Neoteny can thus be one of the determining factors in phylogeny. The logical deduction is that neoteny is a specialization, and, a very important one, which was probably responsible for the evolution of several genera, families, orders, classes and even phyla.

The neotenic features of *Xenopus* listed by MILLARD should therefore be added to those characteristics designated as specializations. It may, however, be that this author separated these two categories of characteristics to indicate those adaptions, which resulted in specializations, in correlation with the aquatic habitat, which itself is a neotenic feature, since the lateral lines are retained (ESCHER, 1925). There is, however, no direct evidence that the characteristics which are frequently considered as "primitive" should not be regarded as neotenic. In fact, the possibility of the origin of *Xenopus* and its relatives by means of total neoteny cannot be denied. It is impossible to accept the view that *Xenopus* is a primitive, or even relatively primitive, anuran. Its retention of an aquatic life is a specialization par excellence and it cannot possibly be maintained that: "Die Tatsache, dasz die Hautsinnesorgane bei Xenopus erhalten geblieben sind weist darauf hin, dasz das Tier niemals im Laufe seiner Phylogenese das Wasser verlassen hat, und deshalb können wir auch erwarten, dasz es Merkmale ursprünglicher Art aufweist" (GROBBELAAR, 1924, p. 168).

The maintenance of an aquatic life and of lateral line sense-organs in the adult were the causative factors leading to further specializations (MILLARD, 1949). These adaptations can be observed in practically every system of the

animal and, with respect to the musculature, they develop very late during metamorphosis.

It cannot be denied that, since the formulation of the theory of neoteny, its significance has been over-emphasized and while one is quite satisfied to accept it as a factor in interpreting groups like the *Acrania* and *Urodela*, it becomes a much more serious matter when the principle is applied to higher chordate groups (DE VILLIERS, 1926). This warning is applicable to *Xenopus* as it is to any other chordate retaining larval characters in the adult. But we have no other alternative explanation to account for certain conditions which obtain in this animal.

Regarding the somatic musculature of the trunk, its development reveals that features of the adult which are supposed to be primitive, actually are specializations, MILLARD (1949) listed three characters of these muscles which were, according to GROBBELAAR, allegedly primitive features. They are: a. the nature of the m. rectus abdominis, stretching from the pelvic region to the hyoid apparatus; b. the m. ileolumbalis not divided into median and lateral portions and c. the general undifferentiated nature of the muscles. As has been very clearly demonstrated previously, this undifferentiated nature of the muscles is secondarily acquired during the latest stages of metamorphosis and during the post-metamorphic period, and must undoubtedly be regarded as an adaptation to the aquatic life. For the same reason the m. ileolumbalis, pars lateralis and medialis are fused in the adult and is a specialization preceded by the more primitive condition in the early post-metamorphic stage. As for many instances this adult feature merely simulates a primitive condition. The posterior attachment of the m. rectus abdominis in *Xenopus* is definitely not primitive. A more primitive condition obtains in the earlier larval stages, where this muscle still reaches the front margin of the medial portion of the pelvic girdle. Its attachment to the epipubis exclusively cannot be regarded as a primitive characteristic for the *Anura*. Even in *Urodela* possessing a similar structure, the ypsiloid apparatus, the m. rectus abdominis is attached both to it *and* to the pelvic girdle. From the above-mentioned evidence it is clear that specializations other than neoteny can simulate primitive conditions.

The interpretation of the presence of a separate m. rectus abdominis superficialis during metamorphosis, and even in the young post-metamorphic stage, is probably the only characteristics of the muscles of the trunk which involves some speculation. In view of our present knowledge of the *Anura*, and of *Xenopus* as a genus, we can readily assume that this is not a primitive feature. It probably simulates a primitive characteristic, and I would suggest that the early post-metamorphic stage is neotenic in respect of the retention of the separate m. rectus abdominis profundus and superficialis. This is a condition which also obtains in terrestrial *Urodela*. In contrast to these, the permanently aquatic urodeles lack a divided rectus muscle, owing to the fusion of the pro-

VOL. 34 1953

fundus, with the superficialis, thus constituting one m. rectus abdominis only (HOFBAUER, 1934). Similarly, the adaptation to an aquatic life in *Xenopus* probably caused the fusion of these two muscles to a single m. rectus abdominis in the adult. The ontogenetic development of the m. rectus abd. in *Xenopus* thus proceeds in exactly the same manner as that of the permanently aquatic *Urodela*, which are known to be neotenic.

The specializations obtaining in the adult *Xenopus*, most of which are environmental adaptations, have already been mentioned in the text. These include the extensiveness of the m. latissimus dorsi, of the pars abdominalis of the m. pectoralis and of the m. transversus abd.; the intimate association of the mm. interarcuales and intertransversarii with the m. longissimus dorsi; the fusion of the following: the m. sternohyoideus and m. rectus abd. superficialis with the m. rectus abd. profundus, the medial and lateral parts of the m. ileolumbalis and the m. coccygeo-sacralis with the m. coccygeo-iliacus; the absence of a pars scapularis of the m. obliquus abd. externus superficialis.

In view of the facts revealed by the study of the ontogenesis of the muscles of the trunk, *Xenopus* must be regarded as a very specialized anuran. In the present state of our knowledge it would appear, that *Xenopus* originated as a totally neotenic animal, and that the larval characteristics which are retained in the adult are those which have always been suitable to an aquatic habitat. Against the background of variation, and through the agency of natural selection, further changes adaptive to water-dwelling conditions have been brought about.

VI. SHORT DESCRIPTION OF THE STAGES OF *XENOPUS*

(As supplied by the Hubrecht Institute)

10 Blastula with first indication of blastopore.
10 ½ Gastrulation.
11 „
11 ½ „
12 „
12 ½ „
13 "Neural groove" stage.
14 Neural plate visible.
15 Neural folds visible
16 Neurulation.
17 „
18 „
19 Neural tube closed.
20 „

21 Suture of neural tube disappears.
22 Beginning of elongation; formation of eye, jaw and gill-primordia.
23 Continuation of these processes.
24 „
25 Beginning of invagination of ear-vesicle.
26 Formation of tail-fin.
27 „
28 Tailbud-stages / Pigmentation of eye.
29 „
30 „
31 „
32 „
33 Beginning of heartbeat / Formation of melanophores.
34 „
35 Initial isolation of gills.
36 „
37 „
38 „
39 Primordal gut begins to shorten.
40 Beginning of gill circulation. Mouth breaks through.
41 Gut starts coiling.
42 Continuation of that process / End of gill circulation about St. 44.
43 „
44 „
45 „
46 Hind-limb-bud visible.
47 Hind-limbs still round / Fore-limbs become visible.
48 „
49 „
50 „
51 Elongation of limb-buds and beginning of blood circulation in them.
52 „
53 "Paddle-stage" hind-limb.
54 "Paddle-stage" fore-limb.
55 Development of the feet and hands and the different subdivision of the extremities.
56 In St. 56 the hand turns into a transverse position.
57 „
57 ½ „
58 Front-leg breaks through the skin (approximate beginning of metamorphosis).
59 Further growth of extremities.

VOL. 34 1953

60 Further growth of extremities.

61 Beginning of reduction of the filterapparatus and the tail-fin. Gill-opening (covered by operculum) much narrower. Head begins to grow narrower. Front-leg starts shifting forward in relation to the heart and the aorta.

62 Opening of operculum only a narrow curved slit.

63 Length of tail reduced to half of total bodylength. Front-leg situated in front of the heart. Operculum closed.

64 Further reduction of the tail.

65 ,,

66 ,,

VII. GENERAL RÉSUMÉ

1. It is important to note that RABL considered the sclerotome of *Amphioxus* to be the homologue of only axial mesenchyme of vertebrates.
2. The axial mesenchyme is of such histogenetical and morphological importance that it must be placed in a separate category to distinguish it from the "mesenchyme" derived from sources other than the sclerotome.
3. It is impossible, when studying the differentiation of the mesenchyme, to distinguish *histologically* between the cells of different origin.
4. The secondary muscles develop by means of proliferations from the primary muscles. These liberated muscle cells are changed into mesenchy*matous* cells, which constitute the anlagen of the myofibrillae.
5. The myofibrillae of the primary muscles develop from epithelial myoblast cells. There is no myoblast stage in the development of the secondary muscles.
6. A possibility that cannot be overlooked, is that the amoeboid mesenchyme cells, participating in the formation of secondary muscles, may be functionally comparable with the osteoclasts found in developing bone.
7. The muscles of the young post-metamorphic *Xenopus* bear a very strong resemblance to those of the adult *Rana*. The only real difference is the greater relative area occupied by the zonal muscles covering the trunk.
8. The first trunk myotome disappears during the pre-metamorphic stage and is thus not included in the adult m. longissimus dorsi.
9. The m. longissimus dorsi is formed from the dorsal part of the original m. dorsalis trunci. Its anterior insertion onto the skull constitutes the fused dorsal portions of trunk myotomes II and III.
10. The m. ileolumbalis of the adult *Xenopus* consists of fused medial and lateral portions, both of which must be considered as separate muscles. The pars medialis (a primary muscle) is a separated ventral portion of the m.

VOL
34
195

dorsalis trunci, whereas the pars lateralis (a secondary muscle) originates from proliferations of the ventro-lateral part of the m. dorsalis trunci, in collaboration with mesenchyme-like cells.

11. The m. coccygeo-iliacus (primary muscle) and the m. coccygeo-sacralis (secondary muscle) are fused in the adult *Xenopus*. The m. coccygeo-iliacus is separated from the postero-ventral part of the m. dorsalis trunci. The m. coccygeo-sacralis arises from the m. dorsalis trunci by means of proliferations. The hindmost m. interarcualis is not incorporated into the m. coccygeo-iliacus.
12. In the young post-metamorphic *Xenopus* the mm. intertransversarii can all be distinguished as such. In the adult they are intimately associated with the m. longissimus dorsi and not with the m. ileolumbalis, pars medialis as in other *Anura* investigated. These secondary muscles arise from the medial face of the m. dorsalis trunci. The m. coccygeo-sacralis represents the hindmost m. intertransversarius.
13. In the adult *Xenopus* the mm. interarcuales are intimately associated with the m. longissimus dorsi. They originate by means of proliferations from the dorso-medial face of the m. dorsalis trunci. During ontogeny ten consecutive pairs can be distinguished, the last pair running between the 9th vertebra and the urostyle.
14. A m. subvertebralis is absent.
15. During ontogeny no indications could be detected of any structures, which could be homologized with a true horizontal myoseptum.
16. The "Urwirbelfortsatz" contains the elements of all the obliquus and rectus muscles of the trunk.
17. The m. rectus abdominis of the adult represents a fusion of the m. rectus abd. profundus and m. rectus abd. superficialis.
18. The occurence of a separate m. rectus abd. superficialis (secondary muscle) in the young post-metamorphic stage is unknown in other *Anura* investigated. Probably this is due to neoteny. Similar conditions obtain in the permanently aquatic urodeles.
19. The m. rectus abd. profundus secondarily takes origin from the epipubis, instead of from the pelvic girdle.
20. There are indications, both in *Xenopus* and in *Ascaphus,* that the muscles of the pelvic girdle do, at least in part, originate from the m. rectus abdominis.
21. The m. sternohyoideus is formed by means of the fusion of two muscle derivatives of the m. rectus abdominis, corresponding to the pars lateralis and pars medialis of *Rana* and *Bufo*. In the adult this secondary muscle is intimately associated with the m. rectus abdominis.
22. Ontogenetic evidence in *Xenopus* indicates that the elements of both the m. obliquus abd. externus and internus are incorporated into the dorsal part (m. obliquus) of the "Urwirbelfortsatz". On its medial side the m. obliquus

abd. gives origin to the m. transversus abd. and on its lateral side to the m. obliquus abd. externus superficialis.

23. The remaining portion of the m. obliquus abd., which disappears during metamorphosis, represents the fused m. obliquus abd. externus profundus and m. obliquus abd. internus.

24. A striking feature of the trunk of the adult *Xenopus* is the large area occupied by zonal muscles such as the m. latissimus dorsi, the m. pectoralis, pars abdominalis and the m. iliacus externus.

25. As regards the origin of the zonal muscles it can readily be assumed, that they are derivatives of the myotome. The possibility cannot be excluded that the pelvic muscles may partially arise from proliferations of the m. rectus abdominis.

26. Neotenic features are to be regarded as specializations in contact to primitiveness. This would imply that, according to the evidence obtained from the ontogenesis of the musculature, *Xenopus* is a very specialized anuran.

27. The maintenance of an aquatic habitat throughout life (which is a neotenic feature) probably is causally responsible for the specialized nature ("adaptations" to water-dwelling conditions) of the muscles of the trunk.

28. The allegedly primitive features of the adult *Xenopus*, such as the attachments of the m. rectus abdominis, the undivided state of the m. ileolumbalis, the absence of a separate m. coccygeo-sacralis and the general undifferentiated nature of the muscles are, on the contrary, all specializations.

29. In the present state of our knowledge it would appear, that *Xenopus* originated as a totally neotenic animal, and that the larval characteristics which are retained in the adult are those which have always been suitable to an aquatic habitat. Against the background of variation, and through the agency of natural selection, further changes adaptive to water-dwelling conditions have been brought about.

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* Not seen in the original.

L.
4
53

IX. ALPHABETICAL LIST OF ABBREVIATIONS USED IN THE FIGURES

ANL.Z.M. Anlage of zonal muscles
ART.S. Articulation surface
AX.M. Axial mesenchyme
BR. Brain
CH. Chorda dorsalis
COR. Coracoid
EPIP. Epipubis
E.V. Ear vesicle
F.D. Fascia dorsalis
F.I.M. Fascia intermuscularis
G. Ganglion
G.A. Gill arch
IL. Ilium
INT.C. Intermediate cells
I.M.F. Intermyotomic fissure
L.A. Linea alba
L.F.M.TR. Longitudinal fibres of m. transversus
L.M.I.TR. Lateral m. intertransversarius
*L.T.M.*II Lateral portion of trunk myotome II
M.C.IL. Musculus coccygeo-iliacus
M.C.SAC. Musculus coccygeo-sacralis
M.D.T. Musculus dorsalis trunci
MED. Medulla spinalis
M.I.AR. Musculus interarcualis
M.IL.E. Musculus iliacus externus
M.IL.P.L. Musculus ileolumbalis, pars lateralis
M.IL.P.M. Musculus ileolumbalis, pars medialis
M.I.TR. Musculus intertransversarius
M.LAT.D. Musculus latissimus dorsi
M.L.D. Musculus longissimus dorsi
M.O. Musculus obliquus abdominis
M.O.E.S. Musculus obliquus abdominis externus superficialis
M.P.P.A. Musculus pectoralis, pars abdominalis
M.R.A. Musculus rectus abdominis
M.R.A.P. Musculus rectus abdominis profundus
M.R.A.S. Musculus rectus abdominis superficialis
M.ST.H. Musculus sternohyoideus
M.S.I. Musculus serratus inferior
M.TR. Musculus transversus abdominis
MYOC. Myocomma
MYOT. Myotome or m. dorsalis trunci
N.A. Neural arch
O.C. Otic capsule
OC.A. Occipital arch

OESO. Oesophagus
PIG. Pigment layer
PR.N. Pronephros
PROC. TR. Transverse process of sacral vertebra
P.T.M. Pre-trunk myotome
RIB 2 Second rib
S.G. Spinal ganglion
S.SC. Suprascapula
ST. Sternum
T.M. Trunk myotome
U.W.F. "Urwirbelfortsatz"
Z.M. Zonal muscle

VOL.
34
1953

THE DEVELOPMENT OF THE CHONDROCRANIUM OF SPHENISCUS DEMERSUS WITH SPECIAL REFERENCE TO THE COLUMELLA AURIS OF BIRDS

BY

A. W. CROMPTON, M.Sc.

(With 38 text-figures)

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L.
4
53

CONTENTS

PART I

I. Introduction 72
II. Material and Technique 73
III. Acknowledgements 74
VI. Description of nine developmental stages 75

A. Stage I
1. The Basal Plate 75
2. The Auditory Capsule 78
3. The Anterior End of the Chondrocranium 79
4. The Palatoquadrate and Meckel's Cartilage 82
5. The Hyoid Arch 83
6. The Branchial Arches 84

B. Stage II
1. The Basal Plate and Auditory Capsule 85
2. The Anterior End of the Chondrocranium 88
3. The Visceral Arches 89

C. Stage III
1. The Basal Plate and Auditory Capsule 91
2. The Anterior End of the Chondrocranium 94
3. The Visceral Arches 96

D. Stage IV
1. The Basal Plate and Auditory Capsule 98
2. The Anterior End of the Chondrocranium 99
3. The Visceral Arches 100

E. Stage V
1. The Basal Plate and Auditory Capsule 101
2. The Orbital Region 104
3. The Ethmoidal Region 105
4. The Visceral Arches 106

F. Stage VI
1. The Basal Plate and Auditory Capsule 107
2. The Orbital Region 109
3. The Ethmoidal Region 110
4. The Visceral Arches 110

G. Stage VII
1. The Basal Plate and Auditory Capsule 111
2. The Orbital Region 112
3. The Nasal Capsule 114
4. The Visceral Arches 116
H. Stage VIII
1. The Basal Plate and Auditory Capsule 116
2. The Orbital Region 118
3. The Nasal Capsule 119
I. Stage IX 120

PART II

I. Résumé and Discussion 122
A. Columella Auris 122
1. Development of the Columella Auris of the Penguin 122
2. Development of the Columella Auris of the Duck 126
3. The Columella Auris of the Fowl, Kestrel, Starling, Nightjar and Ostrich . 126
4. Comparative Anatomical Survey of the two Dorsal processes in the Vertebrate Classes 127
B. The Paraglossum 130
C. The Nasal Capsule and the Os uncinatum 131
D. The Basitrabecular Process, Infrapolar Process and Precarotid commissure . . 134
II. Summary 137
III. References to Literature 140
IV. Alphabetical list of Abbreviations used in the Figures 143

VOL. 34 1953

PART I

I. INTRODUCTION

Apart from the works of W. K. Parker (1866, 1869, 1875 a, 1875 b, 1891 a, 1891 b), T. J. Parker (1892 a, 1892 b), Sushkin (1896, 1899), Tonkoff (1900), Sonies (1907), De Beer and Barrington (1934) and Brock (1937) the avian chondrocranium has not received the same amount of attention as, for example, the reptiles, because it was tacitly assumed that the birds represent "a closed phylogenetic group".

Compared with the chondrocrania of other birds that of the penguin is typically avian. This lends no support to the view of Lowe (1933, 1942) that the penguins arose independently from other birds from a primitive reptilian ancestor devoid of the power of flight. Craigie (1940, 1941) has shown that the cortical structure of the penguin cannot be considered more reptilian than avian. The palatal structure of the penguin skull (Huxley, 1867, Crompton, in press) indicates a close relationship between the penguins and the *Procellariiformes*. Simpson (1946) considers the penguins as a group closely related to the *Procellariiformes* which took directly to "submarine flying" from aerial flight, without the intervention of an intermediate terrestrial stage.

The first part of this paper is devoted to a study of the development of the

chondrocranium and the second is concerned with related morphological problems.

Particular attention has been paid to the development and comparative anatomy of the avian columella auris. Only fragmentary descriptions of the development of this structure in birds have been given by SUSHKIN (1899) for the kestrel, SONIES (1907) for the duck and fowl, SMITH (1905) for the pigeon and DE BEER and BARRINGTON (1934) for the duck. Unfortunately it was not possible to obtain the work of SCHESTAKOWA (1934) on the development of the avian columella auris.

II. MATERIAL AND TECHNIQUE

The penguin embryos for this investigations were collected and sent to me by Mr. W. RAND of the Government Guano Islands. All specimens were fixed in 12 % formalin.

As the age of the embryos could not be ascertained, they were classified according to length (tip of beak to cloacal opening). In many cases, however, this did not prove to be a correct criterion of age, larger embryos proving on microscopical investigation to be younger than smaller ones.

Serial sections were made of a nestling, and embryos of the following lengths: 170 mm., 150 mm., 135 mm., 120 mm., 104 mm., 91 mm., 83 mm., 74 mm., 61 mm., 61 mm., 58 mm., 56 mm., 54 mm., 52 mm., 51 mm., 47 mm., 47 mm., 43 mm. and 34 mm. With the exception of the 56 mm., 54 mm., 51 mm., 47 mm. and 43 mm. embryos, these were all sectioned transversely.

Most young specimens were decalcified in Ebner's solution, while for several of the older embryos concentrated HNO_3 dissolved in 70 % alcohol in the proportion 6: 100 was employed.

The specimens were stained in toto with borax carmine, or Mayer's basic haemalum solution. In the younger stages counterstaining of the sections with azan was not a success, the entire section staining a homogeneous pale blue. The same applied, to a lesser degree, for the older embryos decalcified in Ebner's solution. However, in the older embryos decalcified in alcoholic HNO_3, excellent differential staining was obtained with azan.

In order to concentrate on the staining of cartilaginous tissue the Nowikoff method, redescribed by DE VILLIERS (1922) was employed. The embryo is stained in toto with borax carmine and the sections are counterstained with a strong solution of bleu de Lyon dissolved in 70 % alcohol and an aqueous solution of Bismarck brown. It is essential when employing this technique to control accurately the staining and differentiating times in the different solutions in order to obtain satisfactory results. In some cases, together with Bismarck brown and bleu de Lyon, the sections were lightly stained with carbol fuchsin which

intensifies the brown colour given to the cartilage by Bismarck brown and stains the nerve fibres a light pink. Overstaining with carbol fuchsin should be avoided.

Fairly satisfactory results were obtained with embryos stained in toto with basic haemalum, and the sections stained with Bismarck brown and carbol fuchsin. The employment of carbol fuchsin in the staining technique is particularly helpful in the identification of procartilage. Together with Bismarck brown, this tissue stains a light reddish-brown.

The "projection method" of PUSEY (1939) was employed for the preparation of graphic reconstructions. Further, Pusey's contour method was frequently employed.

To elucidate many difficult features in the cranial morphology, wax-plate reconstruction models were prepared of the skull of the 58 mm. stage, the posterior region of the nasal capsule of the 74 mm. stage, the posterior region of the skull of the 91 mm. stage, the nasal capsule of the 150 mm. stage, and of the columella auris of the duck.

For comparative anatomical details of the avian columella auris, serial sections of a developmental series of the genus *Anas*, sectioned by F. J. GREWE, a young embryo of the South African nightjar (*Nyctisyrigmus pectoralis pectoralis*) sectioned by Dr. M. E. MALAN of the Zoological Institute Stellenbosch, a young embryo of *Stuthio* sectioned by Dr. G. T. BROCK, and a nestling starling sectioned by Prof. C. G. S. DE VILLIERS were available.

By the courtesy of Prof. H. STEINER of the Zoological Institute of Zürich it was possible to study serial sections of a 15 day embryo of the emu (*Dromiceius novaehollandiae*).

VOL. 34 1953

III. ACKNOWLEDGEMENTS

The present investigation was carried out under the supervision of Prof. C. G. S. DE VILLIERS, whom I wish to thank most sincerely for his constant assistance and advice. I am very grateful to Prof. C. A. DU TOIT for his personal interest and valuable criticism, especially during Prof. C. G. S. DE VILLIERS'S absence.

I am further deeply indebted to the Council for Scientific and Industrial Research for a research scholarship, without which this work could not have been undertaken.

To the following I wish to record my cordial thanks: Mr. R. W. RAND, for the collection of penguin material, Prof. STEINER, for serial sections of a 15 day emu embryo, to Mr. D. N. S. VAN EEDEN, for assistance given in the preparation of wax-plate reconstruction models.

CHONDROCRANIUM OF SPHENISCUS DEMERSUS

IV. DESCRIPTION OF NINE DEVELOPMENTAL STAGES

A. STAGE I

(Figs. 1 to 4.)
Total length of embryo: 43 mm.

1. *The Basal Plate*

Arising from the anterior end of the parachordals ("Investing mass" of W. K. PARKER, 1869) is a high transverse bar of cartilage named by SONIES (1907) in the fowl and the duck, the acrochordal plate (*ACR. CAR.*, figs. 1, 2, 3). It forms an angle of approximately 130° with the parachordals; in younger stages this angle is even larger. The blastematous anlages of the acrochordal and the parachordals lie in the same horizontal plane. T. J. PARKER (1892 a) named the acrochordal plate in *Apteryx* the prochordal plate. JAGER (1924) showed that the acrochordal plate arose in connexion with the transverse commissure between the premandibular somites.

Contrary to all birds of which the cranial morphology has been described, the penguin shares a common characteristic with the *Dipnoi, Anura* and *Crocodilia* in that no fenestra basicranialis posterior is present. Although LUTZ (1942) makes no mention of it, no fenestra basicranialis posterior is found in the emu. SONIES (1907), DE BEER and BARRINGTON (1934) and LUTZ (1942) have shown that it is not possible to recognize the paired nature of the parachordals in birds. For this reason DE BEER (1937) suggests the term perichordal plate. However, T. J. PARKER (1892, a and b) claims that in *Apteryx* the parachordals remain distinctly paired until a late ontogenetic stage. Both the acrochordal plate and the perichordal one are traversed by the notochord. The anterior tip of the latter projects forwards a short distance through a small foramen in the anterior surface of the acrochordal plate; this surface is, in reality, its morphological ventral surface.

No attempt has been made in the present paper to investigate the cranial segmentation. However, it is possible in this stage to observe indications of the first and second occipital vertebrae that have become incorporated into the skull. This supports the findings of SONIES (1907), VAN WIJHE (1907, 1910) and DE BEER and BARRINGTON (1934). Three hypoglossal roots (*HYP. ROOTS.*, fig. 1) are present. Lying behind each hypoglossal root is a procartilaginous occipital arch (*OC. ARC.*, figs. 1, 2). These three occipital arches fuse dorsally with one another above the hypoglossal roots to enclose two of the roots in foramina. The anterior hypoglossal root is lodged in a shallow groove in the lateral surface of the basal plate. Later, when the occipital arch corresponding to the segment in front of the first hypoglossal root develops, the latter is also enclosed within a foramen.

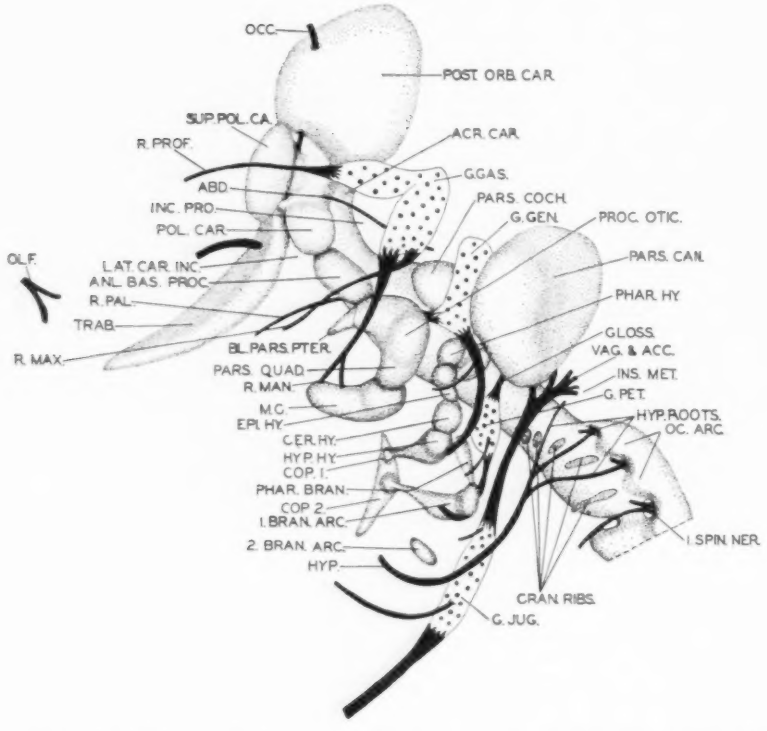


Fig. 1 (X ± 22.2). Stage 1. Reconstruction of chondrocranium and cranial nerves (norma lateralis).

Sushkin (1899) described three hypoglossal nerves in *Tinnunculus*. He claimed that the hypoglossal roots anterior to the posterior three disappeared during ontogeny. Sonies (1907) described only two hypoglossal roots and three hypoglossal foramina in the duck. De Beer and Barrington (1934) claim that up to four hypoglossal roots and five hypoglossal foramina exist in the early ontogeny. De Beer and Barrington's first hypoglossal root is associated with the ephemeral second metotic myomere. If younger stages of the penguin were to be investigated, indications of this first hypoglossal root would no doubt have been encountered. Lutz (1942) described three hypoglossal roots in a 15 day emu embryo, two of which are enclosed in foramina.

A further indication of the cranial segmentation is the presence of 5 cranial ribs (*CRAN. RIBS.*, fig. 1). They appear as areas of dense mesenchymatous tissue separating the myomeres below the perichordal plate. Each cranial rib lies behind the nerve corresponding to its segment. De Beer and Barrington (1934) observed four pairs of cranial ribs in the duck and claim that a connexion exists between the cranial ribs and the metotic cartilage. They, therefore, con-

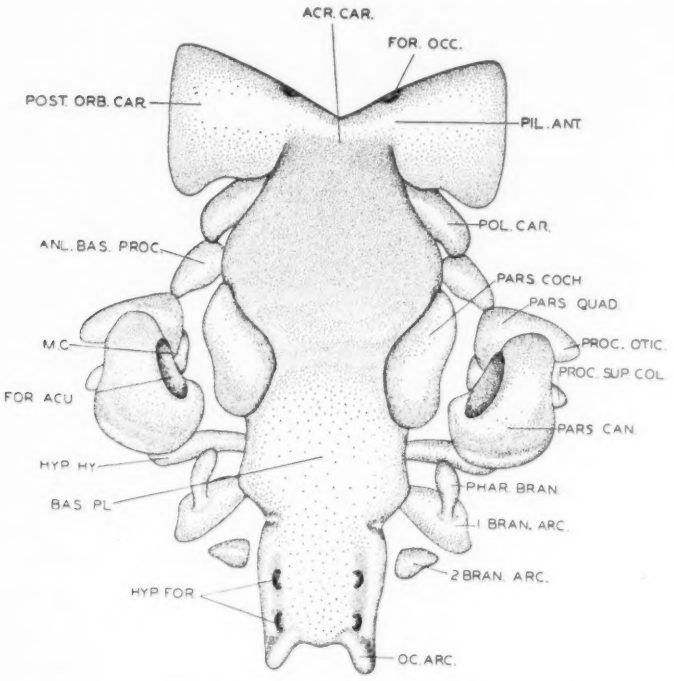


Fig. 2 (X ± 22.2). Stage 1. Reconstruction of chondrocranium (norma dorsalis).

cluded that the metotic cartilage has arisen as the result of fusion of several cranial ribs. SUSHKIN (1899) described four pairs of cranial ribs in the kestrel. SONIES (1907) objects to the homologising of cranial ribs with true ribs, as the former never actually chondrify.

Two large masses of procartilaginous tissue which include the pila antotica (*PIL. ANT.*, fig. 2), (lamina antotica of SONIES, 1907) and the posterior orbital cartilage (*POST. ORB. CAR.*, figs. 1, 2, 3) (alisphenoid of W. K. PARKER, 1866, T. J. PARKER, 1892 a, and PARSONS, 1932) arise on either side from the lateral surfaces of the acrochordal plate. It was not possible to observe the pila antotica and posterior orbital cartilage as two independent structures. However, SONIES (1907) has shown that the pila antotica and the posterior orbital cartilage arise from independent anlages in the fowl. The oculomotor nerve passes downwards between these two anlages. After the fusion of the two anlages in the fowl, the oculomotor nerve is lodged in a shallow groove which indicates the position where the pila antotica and the posterior orbital cartilage meet. In the penguin the oculomotor nerve (*OCC.*, fig. 1) is enclosed in a long canal, which probably represents the border between the posterior orbital cartilage and the pila antotica. An oculomotor canal is also found in *Apteryx* (T. J. PARKER, 1892 a).

2. The Auditory Capsule

The procartilaginous anlage of the pars cochlearis (*PARS. COCH.*, fig. 2) of the auditory capsule, is situated on the latero-dorsal edge of the perichordal plate. Its postero-lateral edge projects laterally past the edge of the perichordal plate to form a shell-shaped roof to the medial region of the cochlear sac. The independence of the pars cochlearis from the perichordal plate supports the view of SONIES (1907) and DE BEER (1937) that the pars cochlearis in an independent structure and not a constituent part of the parachordal, as claimed by W. K. PARKER (1869), T. J. PARKER (1892 a) SUSHKIN (1899) and GAUPP (1900). SONIES named the earliest anlage of the pars cochlearis the cartilago basiotica. According to him it forms the connecting link between the parachordals and the acrochordal plate. In the penguin the pars cochlearis lies too far posteriorly to play the role claimed for it.

The basal plate (*BAS. PL.*, fig. 2) is made up of the following entities; the perichordal plate, the median acrochordal plate and the paired partes cochleares. SUSHKIN failed to observe the constituent parts of the basal plate and for this reason did not consider it to be a composite structure. It was designated by him the "Umhüllungsmasse".

Lateral to and separated from the pars cochlearis by a wide fissure is the procartilaginous anlage of the pars canalicularis (*PARS. CAN.*, figs. 1, 2). It is a cup-shaped structure with a large aperture directed medially. Faint indications of the semicircular canals are observable. The development of the auditory capsule from two independent anlages was observed in the duck by SONIES (1907), and DE BEER and BARRINGTON (1934), and in the starling and the fowl by SONIES (1907).

In the medio-anterior edge of the floor of the pars canalicularis there is a shallow groove lodging the facial nerve (*N.L.7. NER.*, fig. 6). The geniculate ganglion lies dorsal to the cochleo-canalicular fissure. Fused to the medio-ventral surface of the pars canalicularis is the pharyngohyal (*PHAR. HY.*, figs. 1, 4), which in later stages forms the rod and foot-plate of the columella auris. Also in later stages the pharyngohyal ("otostapes") breaks away from the pars canalicularis, with the result that a small circular foramen, the foramen ovale, remains in the side-wall of the pars canalicularis.

In the penguin, therefore, the foramen ovale is situated within the pars canalicularis region of the auditory capsule. SONIES (1907), considers the foramen ovale a remnant of the cochleo-canalicular fissure, while from DE BEER'S (1937) description it is not clear as to whether the foramen ovale develops within the pars cochlearis or pars canalicularis.

Extending ventrally from the latero-posterior edge of the pars canalicularis is a short, blunt procartilaginous process named by SONIES (1907), the cartilago metotica (*MET. CAR.*, fig. 4). He observed that it arose from an independent

anlage in the duck and fowl. De Beer and Barrington (1934) also described the development of the metotic cartilage from an independent cartilaginous anlage in the duck and homologized it with the subcapsular process of the crocodile. As no connexion was observed in the penguin between the widely separated cranial ribs and the metotic cartilage, no support is given to the view of De Beer and Barrington (1934) that the metotic cartilage arises from the fusion of several cranial ribs. Susshkin (1899) named the metotic cartilage the occipital wing and considered it an outgrowth of the "Umhüllungsmasse". T. J. Parker (1892 a) designated the metotic cartilage the "paroccipital process" and considered it an outgrowth of the auditory capsule. In the duck, (De Beer and Barrington, 1934, and Sonies, 1907) the metotic cartilage fuses firstly with the basal plate and secondly with the auditory capsule. In the fowl, (Sonies, 1907) on the other hand, it fuses firstly with the auditory capsule and secondly with the basal plate. In the penguin and in *Apteryx* it develops as an outgrowth of the auditory capsule. In the ostrich (Brock, 1937) the metotic cartilage appears as a tract of mesenchyme continuous with the dorsal edge of the auditory capsule and free ventrally from the lateral edge of the basal plate. As the ontogeny of this structure varies from form to form it is not possible to determine its true nature.

VOL. 34 1953

An extremely wide incisura prootica (*INC. PRO.*, fig. 1), (incisura antotica of Sonies, 1907), is bordered anteriorly by the pila antotica and posterior orbital cartilage, ventrally by the parachordals and pars cochlearis, and posteriorly by the pars canalicularis. The incisura is not completely delimited posteriorly, as the pars cochlearis and pars canalicularis have not yet fused. The ganglion Gasseri (*G. GAS.*, fig. 1) is lodged in the incisura prootica. All the branches of the trigeminal nerve pass outwards through this incisure. The ramus profundus (*R. PROF.*, fig. 1) passes forwards below the posterior orbital cartilage. The abducent nerve (*ABD.*, fig. 1) passes outwards through the most anterior region of the incisura prootica and is not lodged in a notch at the base of the pila antotica as it is in the duck and the fowl (Sonies, 1907).

The incisura metotica (*INC. MET.*, fig. 1) is bordered incompletely anteriorly by the pars canalicularis and pars cochlearis, ventrally by the basal plate and posteriorly by the low occipital arches. The nervus glossopharyngeus (*GLOSS.*, fig. 1) passes downwards immediately behind the pars cochlearis and the composite nerve, (nervus vagus + nervus accessorius: *VAG + ACC.*, fig. 1) passes downwards behind the glossopharyngeus.

3. *The Anterior End of the Chondrocranium*

The polar cartilages (*POL. CAR.*, fig. 1, 3) are fused to the lateral surfaces of the acrochordal plate. Compared with the latter these structures are in an early state of chondrification and, as a result of this, it is possible

to draw a line of demarcation between the two entities. The ventro-lateral region of each polar cartilage is directed ventro-laterally as a short blunt process, which, although it appears on lateral view to simulate an infrapolar process, must not be confused with it. A fairly wide lateral carotid incisure (*LAT. CAR. INC.*, figs. 1, 3) is formed between the acrochordal plate and the trabecular-polar bar. It is traversed by the internal carotids of either side which pass medially to reach the median foramen caroticum (*FOR. CAR.*, fig. 3).

The polar cartilages were first observed by SONIES (1907) in the duck, the starling and the fowl. In the fowl he shows that, as in the penguin, the polar cartilages originate in continuity with the acrochordal plate. According to SONIES (1907) the connexion between the polar cartilages and the basal plate takes place at the border between the pars cochlearis and the acrochordal plate. This is not the case in the penguin, where the partes cochleares lie far behind the acrochordal plate. SUSHKIN (1896, 1899) failed to differentiate the polar cartilages from the trabeculae in the kestrel.

The nature of the polar cartilages has been discussed by several authors. ALLIS (1923, 1924, 1931) claims that they represent pharyngomandibulars. DE BEER (1937) considers that it is possible that the polar cartilages arise from the mandibular arch, but is unable to prove his contention. MATVEIEV (1925) and HOLMGREN (1943) believe that the polar cartilages are of axial origin.

Situated between the ventro-lateral edge of the polar cartilage and the medial surface of the pars quadrata is an oval nodule of dense blastematous tissue, the anlage of the processus basitrabecularis (*ANL. BAS. PROC.*, figs. 1, 2, 3). Its topographical position, lateral to the nervus palatinus, supports the view that it is actually the anlage of this process. In later stages the anlage fuses to the skull base to form a small basitrabecular process. As this anlage occupies the same position as does the pharyngomandibular element in *Selachii*, described by SEWERTZOFF and DISLER (1924), it is not improbable that it represents a pharyngomandibular.

The trabeculae (*TRAB.*, figs. 1, 3) in this stage appear as two independent and widely separated procartilaginous bars. They are flattened in a horizontal plane and lie immediately below the forebrain. The posterior ends of the trabeculae are curved upwards and abut against the anterior surfaces of the polar cartilages. Connecting the posterior ends of the trabeculae with each other across the midline is a faint tract of procartilaginous tissue, the anlage of the precarotid commissure (*PRECAR. COM.*, fig. 3). No mention is made of this commissure in the literature on the avian chondrocranium. Faint indications of it are present in a 15 day emu embryo. LUTZ, however, does not mention it. In the penguin and the emu the large foramen basicranialis anterior is divided into two smaller foramina, a posterior foramen caroticum (*FOR. CAR.*, fig. 3) and an anterior foramen hypophyseos. The foramen caroticum is bordered anteriorly by the precarotid commissure, laterally by the polar cartilages and posteriorly

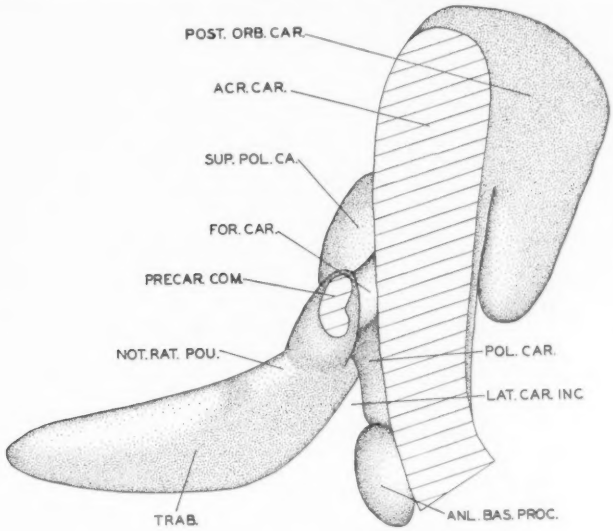


Fig. 3 (X ± 44.4). Stage 1. Topography of the cranial flexure of the penguin.

by the acrochordal plate. The paired carotid arteries from either side pass medially through the lateral carotid incisure and fuse below the median foramen caroticum to form the median internal carotid which passes upwards through the foramen caroticum. Rathke's pouch, lying anterior to the precarotid commissure, passes upwards through the posterior region of the hypophysial fissure (*NOT. RAT. POU.*) which is bordered posteriorly by the precarotid commissure and laterally by the trabeculae. In later stages the trabeculae fuse in front of Rathke's pouch to form the trabecula communis.

The independent origin of the trabeculae was observed in the duck by SONIES (1907), and DE BEER and BARRINGTON (1934). In this stage of the penguin ontogeny the trabeculae are continuous with the polar cartilages, but a clear line of demarcation may be observed between the two structures. The sagittal bar of cartilage dividing the foramen hypophyseos of the sparrow into right and left halves (DE BEER, 1937), is not present in the penguin. HUXLEY (1874), DE BEER (1931, 1937), PLATT (1897), HOWES and SWINNERTON (1901), and ALLIS (1923, 1924, 1931) consider the trabeculae to be of visceral origin. ALLIS went so far as to claim that the trabeculae are homologous with the pharyngopremandibulars. GOODRICH (1930) considers the trabeculae as "structures sui generis developed to support and protect the forebrain and nasal sacs." HOLMGREN (1943) claims that the trabeculae are of axial origin. No attempt has been made in this paper to determine the morphology of the trabeculae. Nevertheless, it is interesting to note that in this stage these cartilages lie practically parallel

VOL. 34 1953

to the other visceral arches. De Beer (1923) considers this fact relevant to this theory that the trabeculae represent the premandibular arches.

Lying above the polar cartilage and the posterior end of the trabecula, is a large nodule of procartilaginous tissue, the anlage of the suprapolar cartilage (*SUP. POL. CA.*, figs. 1, 3). Posteriorly it abuts against the anterior surface of the acrochordal plate, and ventrally it is separated from the trabeculae by a narrow fissure through which the ophthalmic artery passes outwards. The suprapolar cartilages were first observed in the kestrel by Sushkin (1899), who designated them "supratrabecular cartilages". Sonies (1907) pointed out that these structures lie dorsal to the polar cartilages, and for this reason he introduced the term suprapolar cartilages. De Beer (1937) homologizes the suprapolar cartilages with the supratrabecular bar of *Lacerta* and *Sphenodon*.

4. *The Palatoquadrate and Meckel's Cartilage*

The pars quadrata (*PARS. QUAD.*, fig. 1) has a sickle-shaped form. The anlage of the basitrabecular process is syndesmotically connected to the medial surface of the antero-dorsal region of the pars quadrata. No definite corresponding cartilaginous basal process is found upon the pars quadrata. Anterior to the attachment of the basitrabecular process the pars quadrata is continued forward by a short dense blastematous process, the posterior region of the pars pterygoidea (*BL. PARS. PTER.*, fig. 1). In later stages this blastematous process chondrifies in continuity with the pars quadrata to form the processus orbitoquadratus. Anterior to the blastematous processus pterygoidea a faint tract of blastematous tissue extending forward into the ethmoidal region is observable. This probably represents the anterior region of the pars pterygoidea.

Sonies (1907) says the following concerning the processus orbitoquadratus of birds, "— — — und ist mit dem Processus pterygoideus des Palatoquadratums der Reptilien und dem langen Processus palatinus der Knorpel-Fische zu homologisieren". De Beer and Barrington (1934) also consider the processus orbitoquadratus as homologous with the pars pterygoidea, and for this reason employ the term processus pterygoidea for this process. The work of Prins (in press) on the musculus orbitoquadratus of the penguin supports the view, that the processus orbitoquadratus represents a remnant of the pars pterygoidea.

A short blunt process, the processus oticus (*PROC. OTIC.*, figs. 1, 2) arises from the postero-dorsal surface of the pars quadrata and is directed in a latero-dorsal direction. It does not, however, reach the lateral surface of the auditory capsule. Ventrally the pars quadrata is syndesmotically joined to the posterior region of Meckel's cartilage (*M. C.*, figs. 1, 2, 4) which has the form of a short rod. Posteriorly in the region of the pars quadrata it expands laterally.

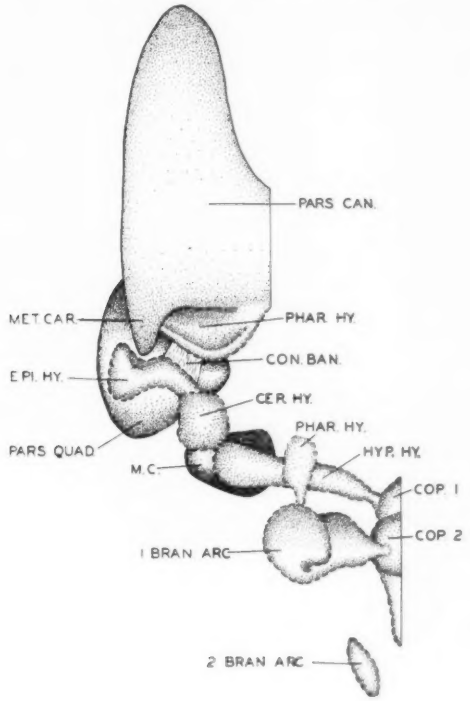


Fig. 4 (X ± 44.4). Stage 1. Reconstruction of hyoid arch (norma posterior).

5. *The Hyoid Arch*

The hyoid arch of this stage is constituted by four blastematous anlages. For the sake of convenience they have been named the pharyngohyal, epihyal, ceratohyal and hypohyal, but, as to whether they are homologous with the similarly named divisions in the piscine hyoid arch, is by no means certain. De Beer (1936) suggests that the visceral arches of fishes and of higher vertebrates may have acquired segmentation independently.

The pharyngohyal (*PHAR. HY.*, figs. 1, 4) appears in syndesmotic continuity with the ventro-medial surface of the pars canalicularis. In later stages the pharyngohyal forms the foot-plate and the major portion of the rod of the columella auris. The epihyal (*EPI. HY.*, figs. 1, 4) lies ventro-caudal to the pharyngohyal. Its lateral region is extended ventro-dorsally past the ventro-lateral surface of the pharyngohyal to form the processus supracolumellaris lateralis (*PROC. SUP. COL. LAT.*, figs. 5, 9). In most birds two dorsal processes, a medial and a lateral, arise from the columella auris. The terms processus supracolumellaris lateralis and medialis have been introduced here to designate these two processes. No processus supracolumellaris medialis is found in the penguin.

The proximal region of the epihyal is connected by means of a tract of con-

nective tissue (*CON. BAN.*, fig. 4) to the ventral edge of the pharyngohyal. Following upon the epihyal in a ventro-caudal and slightly medial direction is a spherical nodule of blastematous tissue, the ceratohyal (*CER. HY.*, figs. 1, 4). A blastematous hypohyal has the form of a long slender rod connecting the ceratohyal to copula 1 (*COP. 1.*, figs. 1, 4).

The ramus hyomandibularis of the facial nerve passes backwards dorsal to the epihyal and medial to the processus supracolumellaris lateralis. Immediately behind the epihyal the chorda tympani is given off from the hyomandibular. This nerve passes forwards lateral to the processus supracolumellaris lateralis. Anterior to the hyoid arch it passes downwards towards the lower jaw.

6. *The Branchial Arches*

Situated medially below the skull and lying almost at right angles to the long axis of the parachordals, is a dense mass of blastematous tissue containing the anlages of copula 1 and 2. These appear as local concentrations within this blastematous mass. SUSHKIN (1899) described a similar condition in the early ontogenetic stages of *Tinnunculus*.

The connexion between the hypohyal (ventral end of the hyoid arch) and copula 1 has not previously been observed in birds, and it indicates that copula 1 is a basihyal.

Behind the hyoid arch and in connexion with copula 2 is the blastematous anlage of the first branchial arch (*1 BRAN. ARC.*, figs. 1, 4). Its attachment to copula 2 indicates that the latter is a basibranchial. W. K. PARKER (1866) considered copula 1 to be part of the hyoid arch and for this reason designated it the "urohyal".

Attached to the postero-dorsal edge of the first branchial arch is a faint tract of blastematous tissue. In later stages it proves to be the site of an independent chondrification which has been named the pharyngobranchial (*PHAR. BRAN.*, figs. 1, 4). This term must not be taken to imply that the anlage is homologous with the piscine pharyngobranchial. No subdivision of the rest of the branchial arch was observed.

A remnant of the second branchial arch (*2 BRAN. ARC.*, figs. 1, 4) of birds in the form of dense blasteme, is found behind the first branchial arch, between the second and third branchial pouches. Whereas in reptiles it develops further, in birds it atrophies in the later ontogeny. KALLIUS (1905) describes a similar condition to that of the penguin in the duck and in the sparrow.

B. STAGE II

(Figs. 5 to 9.)

Total length of embryo: 47 mm.

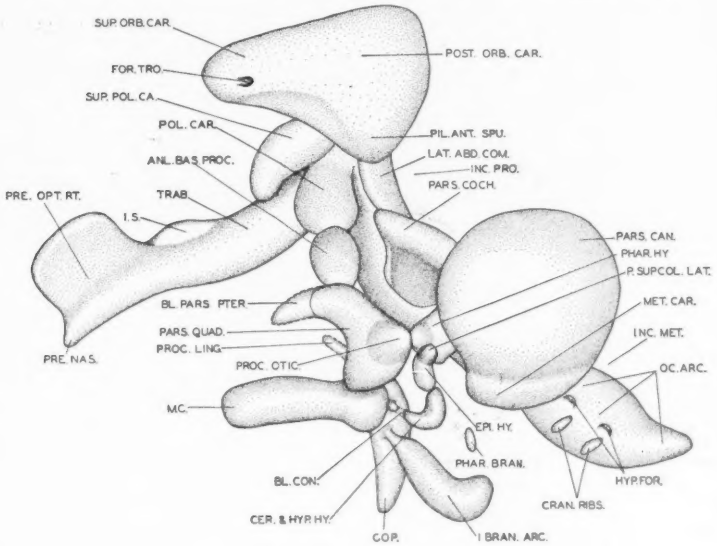


Fig. 5 (X ± 22.2). Stage 2. Reconstruction of the chondrocranium (norma lateralis).

1. *The Basal Plate and Auditory Capsule*

Considerable lateral expansion of the basal plate in the occipital region is observable in this stage. The occipital arch corresponding to the segment in front of the first hypoglossal root has now developed. This arch fuses with the occipital arch behind, dorsal to the hypoglossal root, to enclose the latter in a foramen. The posterior occipital arch has grown in height. In contrast to stage I, where the hypoglossal foramina were directed laterally, they now open in a latero-ventral direction. Only the posterior three cranial ribs of stage I remain.

A blunt process, separating the glossopharyngeal and vagal nerves, arises from the lateral surface of the basal plate, with the result that the nervus vagus is lodged in a shallow depression on the lateral surface of the basal plate (*N. L. 10 NER.*, figs. 6, 7). A similar condition was observed by Sonies (1907) in the duck.

The posterior orbital cartilage has expanded laterally to enclose the trochlear nerve in a long horizontal canal (*FOR. TRO.*, figs. 5, 6, 8). Parsons (1932) observed the trochlear canal in a young embryo the gentoo penguin (*Pygoscelis papua*). The latero-anterior region of the posterior orbital cartilages is extended forwards over the eyes by means of a long procartilaginous process, the supra-orbital cartilage (*SUP. ORB. CAR.*, figs. 5, 6, 8). A flange of slightly differentiated procartilaginous tissue, the anlage of the pila antotica spuria (*PIL.*

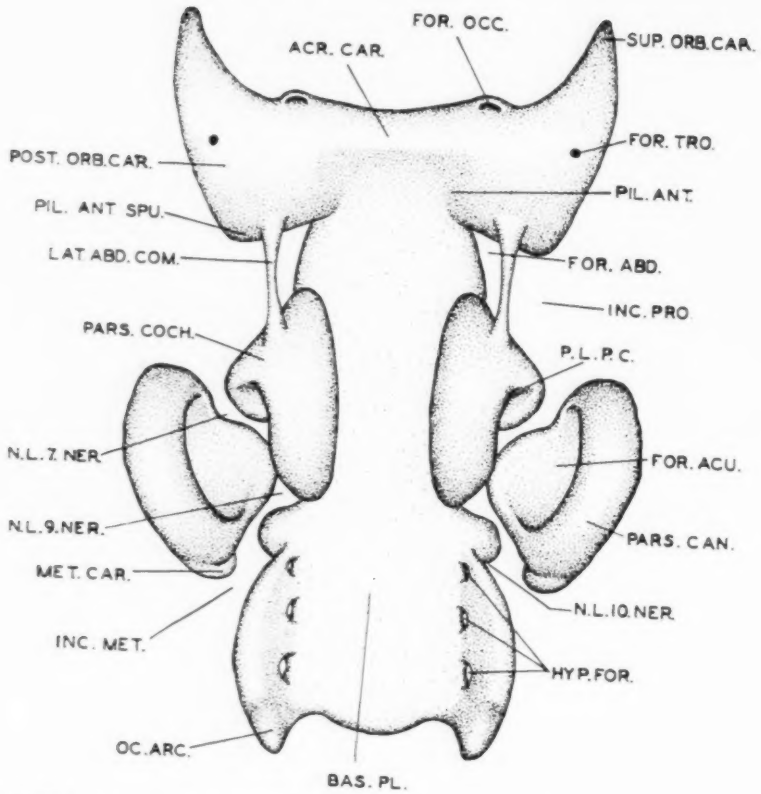


Fig. 6 (X ± 27.5). Stage 2. Reconstruction of basal plate and auditory capsule (norma dorsalis).

ANT. SPU., figs. 5, 6) which lies lateral to the ramus profundus, extends downwards from the latero-ventral region of the posterior orbital cartilage. This supports the findings of De Beer and Barrington (1934) and Brock (1937). Although the presence of a pila antotica spuria is a feature common to most birds, Kesteven (1942) has pointed out that it does not develop in the emu or the grebe (*Podiceps*).

A procartilaginous lateral abducent commissure (*LAT. ABD. COM.*, figs. 5, 6, 7) stretching between the posterior surface of the posterior orbital cartilage and the latero-anterior surface of the pars cochlearis, lateral to the abducent nerve, has developed at this stage. The abducent nerve is now enclosed within its own foramen (*FOR. ABD.*, fig. 6). According to De Beer and Barrington (1934) and Sonies (1907) the abducent foramen is formed by the encroachment of the pila antotica upon the abducent nerve.

It is still possible in this stage to distinguish the pars cochlearis as an in-

VOL. 34 1953

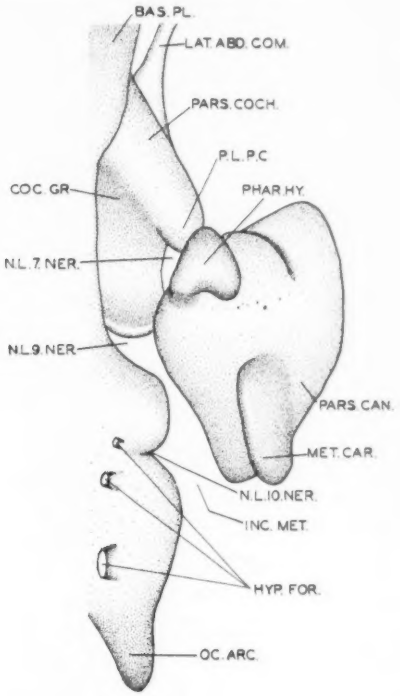


Fig. 7 (X ± 36.6). Stage 2. Reconstruction of auditory capsule (norma ventralis).

dependent structure. As in stage I, it is separated from the pars canalicularis by means of a narrow fissure. The pars cochlearis has increased in length, so that a broader base is apposed to the perichordal plate. The postero-lateral roof of the pars cochlearis has grown further laterally to form an effective roof to the cochlear region of the auditory sac (*COC. GR.*, fig. 7). A short blunt process, the processus lateralis partis cochlearis (*P. L. P. C.*, figs. 6, 7), lying in front of the facial nerve, grows out from the antero-lateral region of the pars cochlearis. The facial nerve passes upwards through the cochleocanalicular fissure towards the geniculate ganglion. A similar course for the facial nerve was described by Brock (1937) in the ostrich. "The facial nerve emerges through a groove situated anteriorly between the cochlear and canalicular portions of the otic capsule, its foramen is not separated from the trigeminal incisure." In later ontogenetic stages of the penguin, the processus lateralis partis cochlearis fuses with the anterior surface of the pars canalicularis and forms an anterior border to the facial nerve foramen. As the pars canalicularis and the pars cochlearis have not yet fused, neither the incisura metotica nor prootica is completely delimited.

The metotic cartilage has increased considerably in size. Its dorsal edge is fused to the latero-dorsal region of the canalicular portion of the otic capsule,

while the ventral edge appears as a broad flange directed in a ventro-medial direction towards the lateral edge of the basal plate. Thus a space, the cavum metoticum, is enclosed between the metotic cartilage, laterally, and the auditory capsule, medially.

2. The Anterior End of the Chondrocranium

It is still possible to distinguish between the trabeculae and the polar cartilages. The medial regions of the polar cartilages are wedged between the trabeculae and the acrochordal plate. Consequently the medial regions of the polar cartilages are narrow, while laterally each expands to form a broad blunt process. With the exception of the narrow distal region, which remains blastematous, the entire blastematous basitrabecular process anlage of the previous stage has chondrified. In the emu and the ostrich the entire anlage of the basitrabecular process chondrifies.

VOL. 34 1953

In stage I the posterior ends of the trabeculae were curved dorsally, so that they lay practically parallel to the acrochordal plate. In the intermediate period between stages I and II the trabeculae have straightened out and rotated dorsally to form a horizontal bar lying practically at right angles to the acrochordal plate. The trabeculae have fused with each other in the midline to form the trabecula communis (*TRAB. COM.*, fig. 8). With the formation of the trabecula communis, the foramen hypophyseos (*FOR. HYPOP.*, fig. 8). is now completely delimited.

T. J. Parker (1892 a, and b) described three basicranial foramina in the skullbase of *Apteryx:* a posterior, a middle and a anterior basicranial foramen. The anterior two appear to be homologous with the foramen hypophyseos and the foramen caroticum of the penguin. The boundary between the two foramina is formed in *Apteryx* by a commissure connecting the posterior regions of the trabeculae. Anteriorly the trabecula communis is extended forwards as a short prenasal process (*PRE. NAS.*, figs. 5, 8). Two flat plates of procartilaginous tissue, the preoptic roots of the orbital cartilage (*PRE. OPT. RT.*, figs. 5, 8) directed dorsally and slightly laterally, arise from the antero-lateral surfaces of the trabecula communis. The interorbital septum (*I. S.*, figs. 5, 8) grows upwards from the centre of the trabecula communis behind the preoptic roots. Brock (1937) in her description of the ostrich chondrocranium claims that the interorbital septum is formed by the fusion of the preoptic roots with each other in the midline. The present, and the later ontogenetic stages of the penguin clearly show that the interorbital septum and the preoptic roots are two distinct structures. The preoptic roots may in later ontogenetical stages be cemented to the anterior region of the interorbital septum, but they certainly do not represent the latter.

W. K. Parker (1891), Sushkin (1899), and Filatoff (1906) claim the

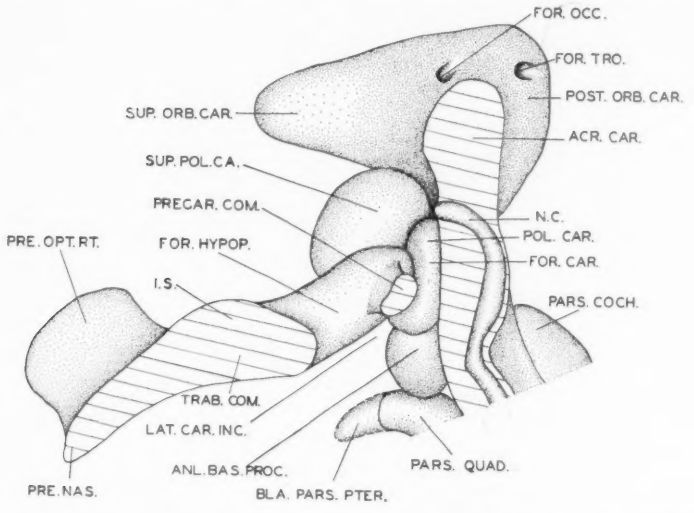


Fig. 8 (X ± 30). Stage 2. Topography of the cranial flexure of the penguin.

existence of an intertrabecular bar in the fowl, kestrel and pigeon respectively. According to these authors the interorbital septum develops out of this structure. No indication of an intertrabecular bar is found in the penguin. The trabeculae fuse with each other without the intermediation of an intertrabecular bar to form the trabecula communis. Although the central tissue constituting the trabecula communis is in a less advanced state of chondrification than the laterally situated tissue, this central portion cannot be considered a separate structure.

3. *The Visceral Arches*

The processus oticus of the pars quadrata has increased considerably in length, but it has not yet reached the auditory capsule. The pars pterygoidea is still in a blastematous condition. Meckel's cartilage has increased in length.

The blastematous pharyngohyal has grown in an antero-medial direction to form a short blunt process. In later stages this will constitute the major part of the columella auris rod. The blastematous processus supracolumellaris lateralis is directed in a more dorsal direction than in the previous stage. Continuous with the dorsal end of this process is a nodule of blastematous tissue (not shown in the reconstruction) lying between the processus oticus and the metotic cartilage. This nodule is probably homologous with the intercalary of reptiles. The increased growth of the pharyngohyal has shortened the distance separating the pharyngohyal and the epihyal.

In the rest of the hyoid arch the ceratohyal and the hypohyal have fused to

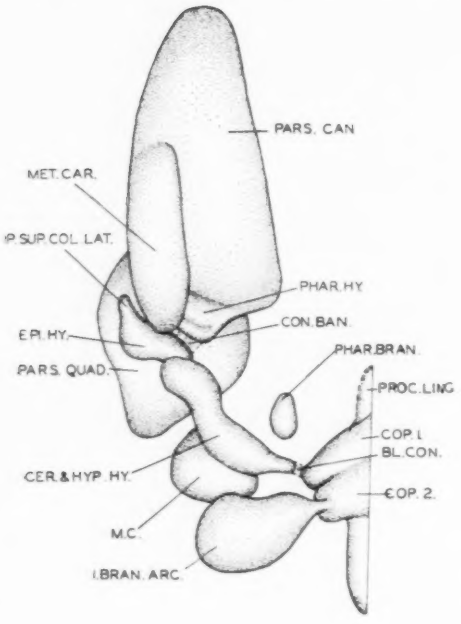


Fig. 9 (X ± 36.6). Stage 2. Reconstruction of the hyoid arch (norma posterior).

form a long blastematous rod. The slender connexion formerly existing between the hyoid arch and the basihyal, has atrophied so that only a faint tract of blasteme (*BL. CON.*, fig. 9) remains to indicate its earlier presence.

Copula 1 and 2 have chondrified to form a single copula, but a demarcation may still be observed between the two structures. A short, blunt process directed towards the ventral end of the hyoid arch arises from the lateral surface of copula 1. KALLIUS (1905) named this process the lateral wing of the copula. Copula 1 is extended forward by a blastematous process (*PROC. LING.*, figs. 5, 9). It is not improbable that this process is homologous with the processus lingualis of reptiles and the "glossohyal" (SUSHKIN, 1899). In later stages it atrophies, and the anlage of the paraglossum develops dorsally to it. It was not found possible to ascertain whether any part of the processus lingualis contributes to the formation of the paraglossum.

The first branchial arch is still in a blastematous state. Proximally it has a slender attachment to a short, laterally directed process of copula 2 (basibranchial). This process is serially homologous with a similar process on the lateral surface of the basihyal. The blastematous pharyngobranchial is found occupying the same position as it occupied in stage I. However, as a result of the extensive backward growth of the first branchial arch, the previous slender connexion between the two structures is broken down.

The blastematous second branchial arch has atrophied.

VOL. 34 1953

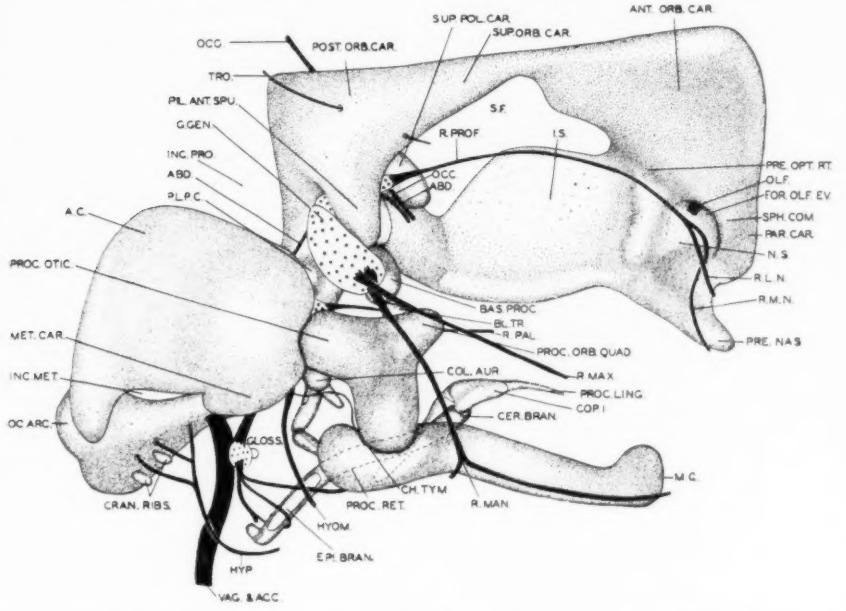


Fig. 10 (X ± 20.5). Stage 3. Reconstruction of chondrocranium and cranial nerves (norma lateralis).

C. STAGE III

(Figs. 10 to 13.)

Total length of embryo: 56 mm.

A large gap in the development exists between stages II and III but, despite this, the advance from the former to the latter may be accurately followed.

1. *The Basal Plate and Auditory Capsule*

The occipital region of this stage is characterized by the extensive growth of the posterior occipital arch. It rises steeply from the posterior region of the basal plate to form a high posterior wall to the fissura metotica.

In this stage four hypoglossal foramina are found in the left side of the basal plate. No hypoglossal nerve traverses the anterior hypoglossal foramen. Only the two posterior cranial ribs remain in this stage.

The laterally directed process of the basal plate anterior to the nervus vagus has fused with the basal plate behind the nervus vagus to enclose the latter within its own foramen (*FOR. VAG.*, figs. 10, 11, 12). The metotic cartilage plays no role in the formation of this foramen. De Beer and Barrington (1934) claim that, in the duck, the fissura metotica is divided into two by the metotic

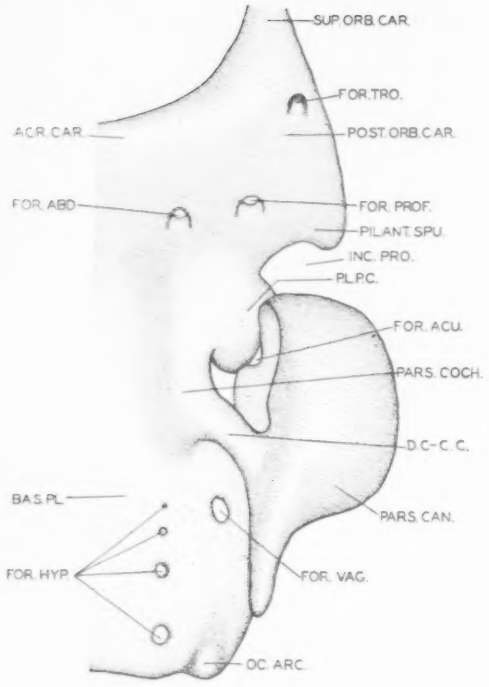


Fig. 11 (X ± 27.3). Stage 3. Reconstruction of basal plate (norma dorsalis).

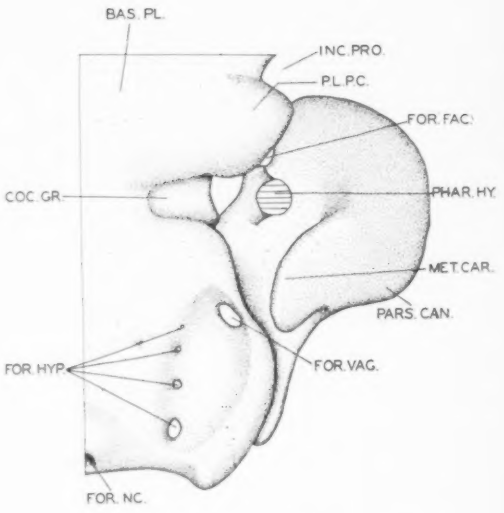


Fig. 12 (X ± 27.3). Stage 3. Reconstruction of auditory capsule (norma ventralis).

cartilage which fuses with the basal plate between the nervus vagus and the nervus glossopharyngeus. They do not make it clear whether the nervus vagus is enclosed within a foramen in the basal plate or whether it passes outwards through a remnant of the fissura metotica. According to SONIES' (1907) description for the duck, the metotic cartilage fuses with the basal plate behind the notch lodging the nervus vagus and then spreads forwards to cover the groove laterally. BROCK (1937) claims that in the ostrich both the nervus vagus and the nervus glossopharyngeus are surrounded by the metotic cartilage.

Above the eyes a slender connexion is developed in this stage between the supraorbital cartilage and the anterior orbital cartilage. The anterior surface of the posterior orbital cartilage presents a concave surface to the posterior surface of the eye-ball.

The pila antotica spuria is now fully formed; below the ramus profundus it fuses with the lateral abducent commissure to enclose the ramus profundus in its own foramen (*FOR. PROF.*, fig. 11). An independent foramen for the ramus profundus was observed in *Apteryx* by T. J. PARKER (1892 a) and in the fowl and the duck by SONIES (1907). DE BEER and BARRINGTON (1934), who

VOL. 34 1953

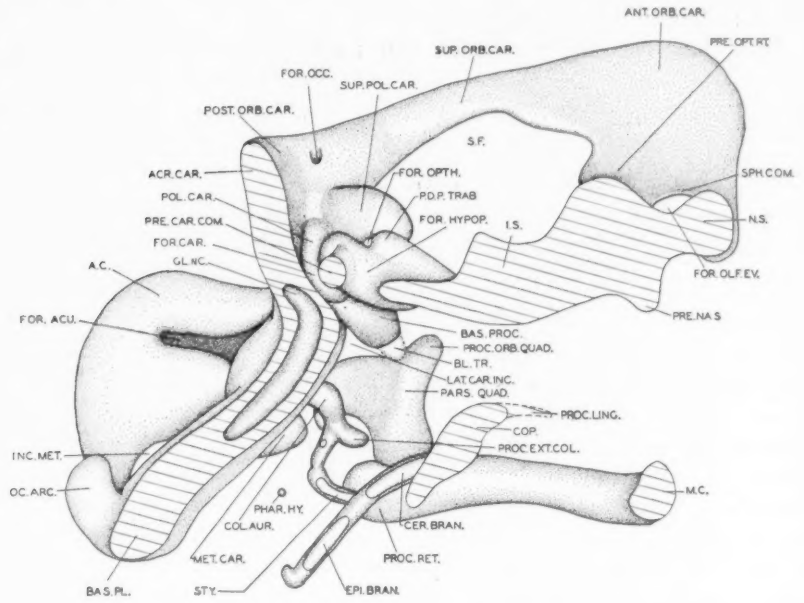


Fig. 13 (X ± 27.3). Stage 3. Disposition of cranial entities as viewed from a median sagittal section.

described the development of the pila antotica spuria in the duck, were the first to realize its significance.

The anterior wall of the oculomotor canal now appears as a thin cartilaginous lamella. This clearly indicates that the anterior wall is undergoing degeneration.

Fusion between the lateral abducent commissure and the basal plate behind the abducent nerve has considerably reduced the size of the foramen for the abducent nerve.

The partes cochleares have now fused completely with the perichordal plate. Further, the perichordal plate has extended laterally to fuse with the free latero-posterior region of the pars cochlearis, forming a roof to the cochlear region of the auditory sac. All that now remains to indicate the presence of the partes cochleares are two shallow grooves in the ventral surface of the basal plate. The grooves lodge the cochlear sacs of either side. The processus lateralis partis cochlearis has grown further laterally to abut against the pars canalicularis. The dorsal surface of this process is syndesmotically fused to the antero-ventral surface of the pars canalicularis in front of the facial nerve. The posterior surface of this process abuts against the ventral floor of the pars canalicularis postero-medial to the groove lodging the facial nerve. As a result the facial nerve is wedged between the processus lateralis partis cochlearis and the canalicular portion of the otic capsule (*FOR. FAC.*, figs. 11, 12, 14). That

part of the processus lateralis partis cochlearis lying in front of the facial nerve may be considered homologous with the prefacial commissure described by De Beer and Barrington (1934) for the duck. In the young ontogenetic stages of the penguin the facial nerve has to pass through the cavity of the auditory capsule in order to reach the geniculate ganglion.

A broad cartilaginous commissure stretches between the postero-dorsal region of the pars cochlearis and the ventro-lateral surface of the pars canalicularis. The term dorsal cochleo-canalicular commissure (*D. C.-C. C.*, figs. 11, 14) has been introduced in this paper to designate this commissure.

The fusion of the processus lateralis partis cochlearis with the pars canalicularis anteriorly, and the development of the dorsal cochleo-canalicular commissure posteriorly, form the anterior and posterior borders of the acustic foramen (*FOR. ACU.*, figs. 11, 13, 14), the lateral border of which is formed by the pars canalicularis, and the medial, by the pars cochlearis. The acustic foramen must therefore be considered a remnant of the cochleo-canalicular fissure. With the fusion of the two regions of the otic capsule with each other, the posterior border of the incisura prootica and the anterior border of the incisura metotica are now completed.

The pars canalicularis is extended backwards as a broad conical process lying above the basal plate. The metotic cartilage has grown further in a medio-ventral direction towards the basal plate.

2. *The Anterior End of the Chondrocranium*

In this stage the polar cartilages are indistinguishably fused to the trabeculae anteriorly, and to the acrochordal plate posteriorly. The anlage of the basitrabecular process is fused to the antero-ventral surface of the polar cartilage, but a line demarcating the two entities is still observable. A tract of blastematous tissue (*BL. TR.*, figs. 10, 13, 14) still connects the basitrabecular process (*BAS. PROC.*, figs. 10, 13, 14) with the pars quadrata.

The ventral region of the acrochordal plate has migrated forwards to come to lie beneath the polar cartilage. As a result, the formerly wide, lateral carotid incisure has been narrowed down considerably.

Fusion between the suprapolar cartilage and the trabeculo-polar bar has enclosed the ophthalmic artery in a small foramen (*FOR. OPTH.*, fig. 13). In front of the ophthalmic artery the suprapolar cartilage fuses with a postero-dorsally directed process of the trabeculae (*P.D.P. TRAB.*, fig. 13). Behind the ophthalmic artery the suprapolar cartilage fuses with the dorsal surface of the polar cartilage and the anterior surface of the acrochordal plate. The ventral opening of the oculomotor canal lies laterally to the upper end of the suprapolar cartilage.

VOL. 34 1953

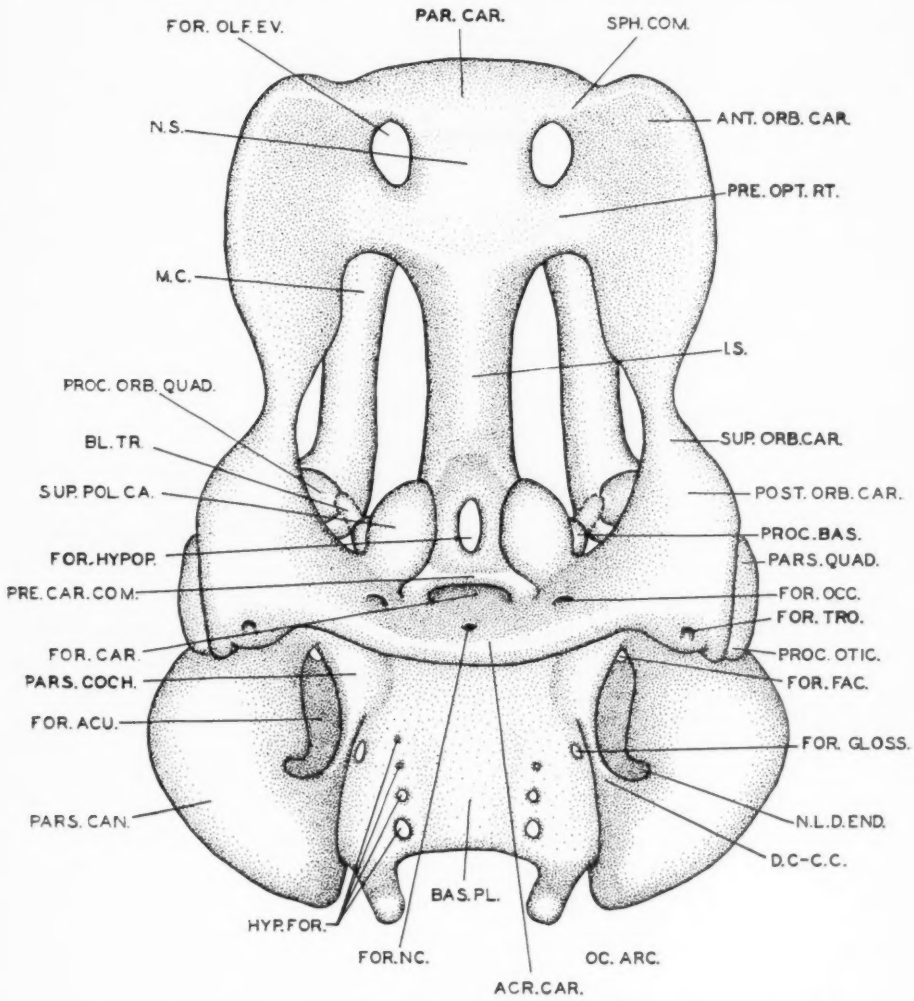


Fig. 14 (X ± 25). Stage 3. Reconstruction of chondrocranium (norma dorsalis).

As a result of the degeneration of the tubular duct connecting Rathke's pouch to the stomodaeum, the hypophysial foramen has begun to close.

The prenasal process, seen for the first time in Stage II, has greatly increased in length. Appearing as a new structure in this stage is the nasal septum (*N. S.*, figs. 10, 13, 14). It is formed as an upward growth of the postero-dorsal surface of the prenasal process, and is continuous with the interorbital septum behind. At its base the septum is narrow, but dorsally it expands sidewards to form the parietotectal cartilage (*PAR. CAR.*, figs. 10, 14). Consequently the nasal septum seen in transverse section presents a triangular shape. The inter-

orbital septum has increased considerably in height, mainly between the preoptic roots. A transverse section of this stage shows that the preoptic roots arise from the lateral surface of the trabecula communis and extend upwards, parallel to the interorbital septum. At a point level with the upper end of the septum, the preoptic roots expand into two large cartilaginous plates, the anterior orbital cartilages (*ANT. ORB. CAR.*, figs. 10, 13, 14), (orbitosphenoids of T. J. PARKER, 1892 a). These cartilages extend backwards, lateral to, but widely separated from, the interorbital septum, to achieve a slender connexion with the posterior orbital cartilage. A large sphenoid fontanelle (*S. F.*, figs. 10, 13) is now enclosed on each side, through which the optic nerves pass outwards. With the interorbital septum as a base and the orbital cartilages as the side walls, a deep trough is formed which lodges the forebrain.

A sphenethmoid commissure (*SPH. COM.*, figs. 10, 13, 14) has developed connecting the anterior surface of the orbital cartilage with the parietotectal cartilage of the nasal capsule. This commissure forms the lateral border of the foramen olfactorium evehens (*FOR. OLF. EV.*, figs. 10, 13, 14), which is further bordered medially by the nasal septum, posteriorly by the preoptic root and anteriorly by the posterior edge of the parietotectal cartilage. The nervus olfactorius passes through the foramen olfactorium evehens to reach the nasal sac. Below the large foramen olfactorium evehens, the ramus profundus divides into two branches; the ramus medialis nasi and the ramus lateralis nasi. While the ramus medialis nasi passes downwards alongside the medial surface of the nasal septum and follows the prenasal process forwards, the ramus lateralis nasi passes forwards in an antero-lateral direction. It will be seen in later stages that the ramus medialis nasi passes through the cavity of the nasal capsule.

3. *The Visceral Arches*

In the pars quadrata, the processus oticus has reached, and articulates with, the auditory capsule and the antero-dorsal surface of the metotic cartilage. The blastematous pars pterygoidea has chondrified in continuity with the pars quadrata to form the processus orbitoquadratus (*PROC. ORB. QUAD.*, figs. 10, 13, 14).

Meckel's cartilage has increased considerably in length; it extends backwards beyond the pars quadrata to form the processus retro-articularis (*PROC. RET.*, fig. 10).

Extensive changes have taken place in the hyoid arch. The epihyal and pharyngohyal elements have chondrified and fused to form the columella auris (*COL. AUR.*, figs. 10, 13), and the pharyngohyal now exists in cartilaginous continuity with the pars canalicularis. The processus supracolumellaris lateralis has chondrified, and the blastematous intercalary has atrophied. Of particular

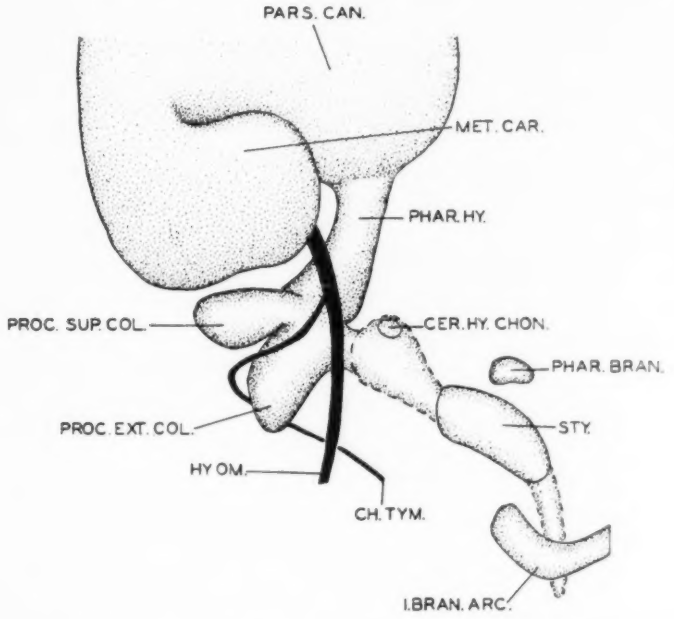


Fig. 15 (X ± 66.6). Stage 3. Reconstruction of the hyoid arch (norma posterior).

importance in this stage is the development of the processus extracolumellaris (*PROC. EXT. COL.*, figs. 13, 15). It develops from the base of the epihyal and is directed in an antero-ventral and slightly lateral direction. Following upon the proximal region of the epihyal, in a medio-ventral direction, is the rest of the hyoid arch which is still to a large extent in a blastematous state. The connexion between the ventral end of the hyoid arch and copula 1 has atrophied completely. When the hyoid cornu is viewed from the lateral aspect, it presents a semicircular shape with both the dorsal and ventral extremities directed forwards. Within the blastematous hyoid cornu two centres of chondrification may be observed. One of these (*CER. HY. CHON.*, fig. 15) is found in the dorsal region of the cornu, and from its topographical position it may be concluded that it represents a chondrification of the ceratohyal blasteme. Similarly the chondrification in the ventral region of the hyoid cornu appears to be a chondrification of the hypohyal blasteme. This chondrification is generally designated as the "stylohyal" (*STY.*, figs. 13, 15). In several birds, for example the duck and the fowl, the entire hyoid cornu chondrifies from a single centre. The chorda tympani in its forward course from behind the columella auris passes lateral to the processus supracolumellaris lateralis and dorsal to the processus extracolumellaris.

During the intervening development, between stages II and III, the median

copula has migrated forwards and has come to lie below the trabeculae. The processus lingualis is still in a blastematous condition.

Within the blasteme of the first branchial arch two centres of chondrification are present, the ceratobranchial (*CER. BRAN.*, figs. 10, 13) and the epibranchial (*EPI. BRAN.*, figs. 10, 13). W. K. PARKER (1866) originally named these two divisions of the branchial arch the "thyrohyals" but, in a later work (1869), introduced the terms ceratobranchial and epibranchial. Most of the modern workers on the avian chondrocranium employ PARKER'S (1869) terminology. However, GAUPP (1900) homologized the divisions of the avian branchial arch with those of the *Urodela* and consequently designated them hypo- and ceratobranchials. According to KALLIUS (1905), the cerato- and epibranchials arise in the duck by segmentation of a solid cartilaginous branchial arch. This is contrary to the findings of SONIES (1907), and DE BEER and BARRINGTON (1934), who describe the branchial arch of the duck as developing from two independent cartilaginous centres. As no subdivision was observed in the penguin branchial arch in the blastematous state, PARKER'S (1869) terminology will be retained.

The blastematous pharyngobranchial has now chondrified and appears as a small nodule lying close to the geniculate ganglion. A dorsally directed blastematous process situated at the extreme distal end of the first branchial arch is reminiscent of the earlier ontogenetic connexion between the pharyngobranchial and the rest of the first branchial arch.

VOL 34 195

D. STAGE IV

(Figs. 16 and 17.)

Total body length of embryo: 51 mm.

Although this stage is somewhat smaller than the previous one its development is slightly more advanced.

1. *The Basal Plate and Auditory Capsule*

The incisura metotica is almost completely obliterated in this stage by the fusion of the auditory capsule with the basal plate below, and with the occipital arch behind. Only the anterior region of the recessus scalae tympani (*REC. SCA. TYM.*, fig. 21), through which the nervus glossopharyngeus passes outwards, remains. The fusion between the two regions of the auditory capsule has proceeded further. Anteriorly it is no longer possible to distinguish between the processus lateralis partis cochlearis and the pars canalicularis. In addition, a further cartilaginous commissure has developed connecting the postero-ventral surface of the pars cochlearis with the ventral surface of the pars canalicularis. The term ventral cochleo-canalicular commissure (*V. C.-C. C.*, fig. 21) has been introduced here to designate this commissure; it lies vertically below the

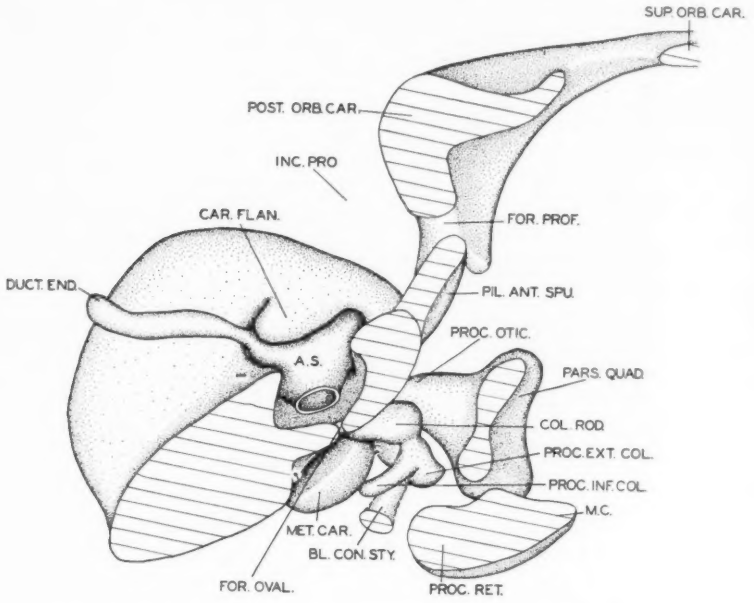


Fig. 16 (X ± 23.3). Stage 4. Topography of the suspensorial region.

dorsal cochleo-canalicular commissure. With the development of the ventral commissure the foramen perilymphaticum (*FOR. PER.*, figs. 20, 21) is delimited. It is bordered dorsally and ventrally by the dorsal and ventral cochleo-canalicular commissures respectively, laterally by the pars canalicularis and medially by the pars cochlearis. Anteriorly this foramen opens into the cavity of the auditory capsule, and posteriorly into the recessus scalae tympani.

A cartilaginous flange (*CAR. FLAN.*, fig. 16) now grows downwards from the central portion of the lateral edge of the auditory foramen, medial to the ductus endolymphaticus (*DUCT. END.*, fig. 16). As a result, the ductus endolymphaticus is lodged in a deep notch in the posterior corner of the auditory foramen.

In this stage the first indications of the foramen ovale (*FOR. OVAL.*, fig. 16) can be observed. Anteriorly and posteriorly to the proximal region of the pharyngohyal, the cartilaginous wall of the pars canalicularis has begun to atrophy. The lateral and medial portions of the pharyngohyal are still fused to the otic capsule.

2. *The Anterior End of the Chondrocranium*

As a result of further increase in height of the interorbital septum, the sphenoid fontanelle is smaller. In this stage the maximum development of the supra-

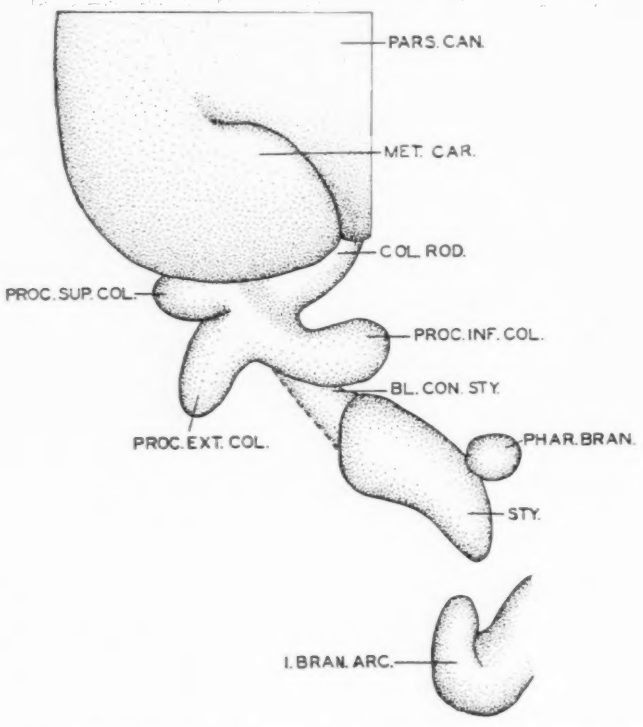


Fig. 17 (X ± 55). Stage 4. Reconstruction of the hyoid arch (norma posterior).

orbital cartilage is encountered. It appears as a broad horizontal plate underlying the forebrain.

3. *The Visceral Arches*

In the hyoid arch the ceratohyal cartilage has fused to the medial surface of the epihyal. Further, the medial region of the ceratohyal has extended medially as a short blunt process to form the processus infracolumellaris (*PROC. INF. COL.*, fig. 17). A blastematous connexion (*BL. CON. STY.*, fig. 17) is still found between the stylohyal and the columella auris. In most birds the processus infracolumellaris is considered to represent a remnant of the earlier connexion between the hyoid cornu and the columella auris. This is not the case in the penguin, in which the processus infracolumellaris is found together with the above connexion.

E. STAGE V

(Figs. 18 to 22.)

Total length of embryo: 58 mm.

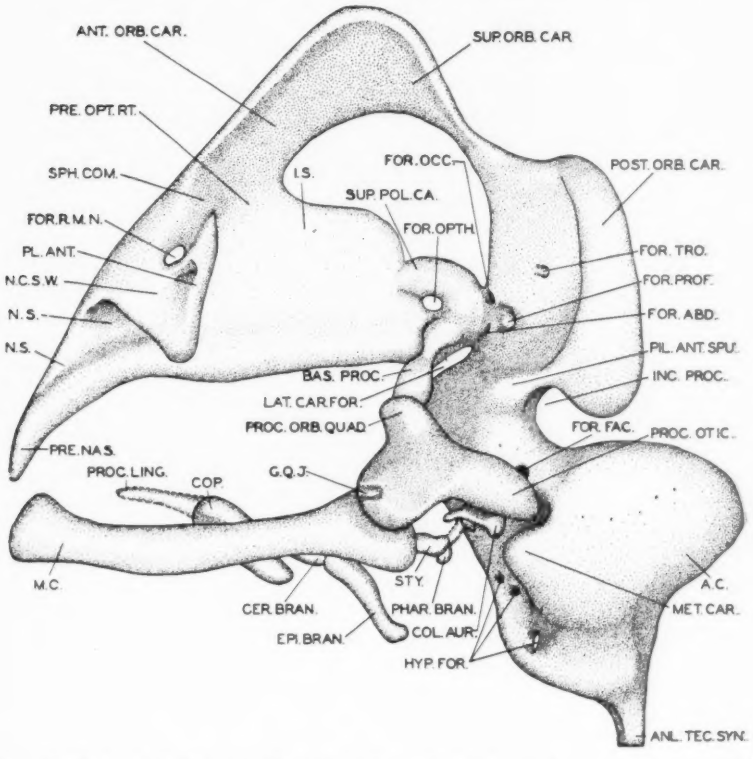


Fig. 18 (X ± 16.2). Stage 5. Reconstruction of chondrocranium (norma lateralis).

As a result of the extensive development of the ethmoidal region, the skull is now beginning to assume a typical avian appearance.

1. *The Basal Plate and Auditory Capsule*

The posterior orbital cartilage has grown considerably sideways and upwards to form a thick transverse concave plate forming the posterior wall to the orbit. Together with the above-mentioned growth, a corresponding degeneration of the anterior and posterior regions of the posterior orbital cartilage has taken place. The lateral expansion of the posterior orbital cartilage is well illustrated by the position of the trochlear canal. Whereas in the previous stages it was lying near the lateral surface, it now lies relatively nearer the medial surface. The supraorbital cartilage has atrophied, so that only a slender connexion remains between the two regions of the orbital cartilage. The oculomotor nerve is still covered by a thin strip of cartilage.

A blastematous tract, the anlage of the tectum synoticum (*ANL. TEC. SYN.*,

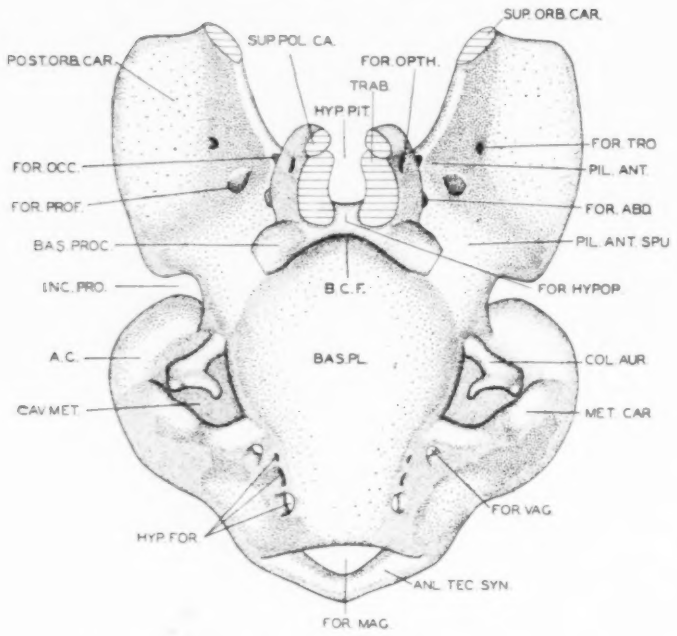


Fig. 19 (X ± 16.6). Stage 5. Reconstruction of the basal plate (norma ventralis). The anterior region of the chondrocranium has been removed.

figs. 18, 19, 21), connects the posterior ends of the auditory capsule with each other behind the medulla oblongata to form the posterior border for the foramen magnum (*FOR. MAG.*, figs. 19, 21).

In this stage the postero-lateral edge of the posterior orbital cartilage closely approaches the dorsal surface of the auditory capsule, with the result that the wide incisura prootica has been narrowed down considerably.

In the auditory capsule a cartilaginous plate has developed which forms the floor to the cochlear groove. Laterally this floor is continuous with the pars canalicularis. All that now remains to indicate the double origin of the auditory capsule is the position of the foramen for the facial nerve. This nerve still passes through the cavity of the auditory capsule, but there is a tendency for it to be enclosed in a canal formed by the further fusion of the two regions of the auditory capsule behind the facial nerve.

The flange of cartilage which was lying medially to the ductus endolymphaticus, has fused with the dorsal cochleo-canalicular commissure so as to form a separate foramen for the ductus endolymphaticus. The auditory foramen now assumes a circular shape.

The recessus scalae tympani opens medially into the cranial cavity through the apertura medialis recessus scalae tympani (*A. M. R. S. T.*, figs. 20, 21) and

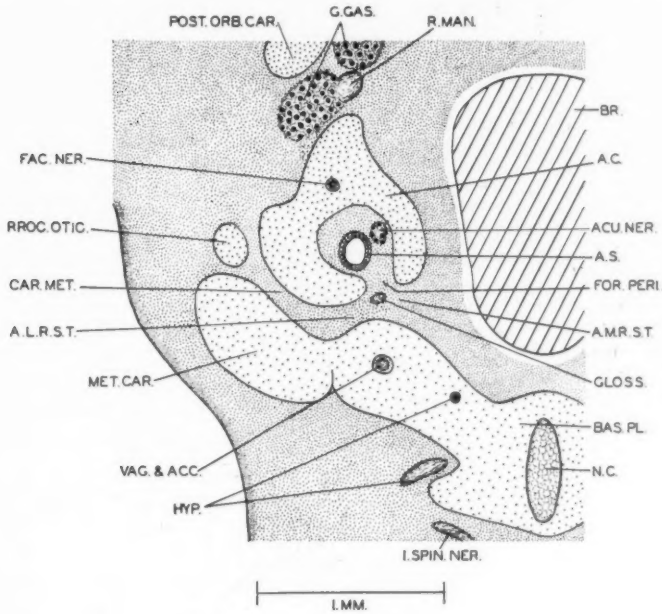


Fig. 20. Stage 5. Transverse section through the auditory capsule.

laterally into the tympanic cavity through the apertura lateralis recessus scalae tympani (*A. L. R. S. T.*, fig. 20).

In earlier stages a growth of the metotic cartilage towards the lateral edge of the basal plate was observed, but in this stage the metotic cartilage has fused with the lateral edge of the basal plate, lateral to the fusion of the auditory capsule with the basal plate.

In the penguin therefore, the metotic cartilage plays no role in the dividing up of the fissura metotica. The posterior edge of the metotic cartilage has fused to the lateral surface of the auditory capsule, while the thick anterior edge remains free and forms a lateral wall to the apertura lateralis recessus scalae tympani. The cavum metoticum opens forwards into the tympanic cavity. The medial region of the metotic cartilage is continued forwards as the subcapsular process, which fuses to the lateral edge of the basal plate, thereby forming a floor to the recessus scalae tympani. In birds only does the recessus scalae tympani possess a floor. The secondary tympanic membrane is stretched over the fenestra pseudorotunda, which is bordered dorsally by the ventral edge of the foramen perilymphaticum and ventrally by the lateral edge of the subcapsular process.

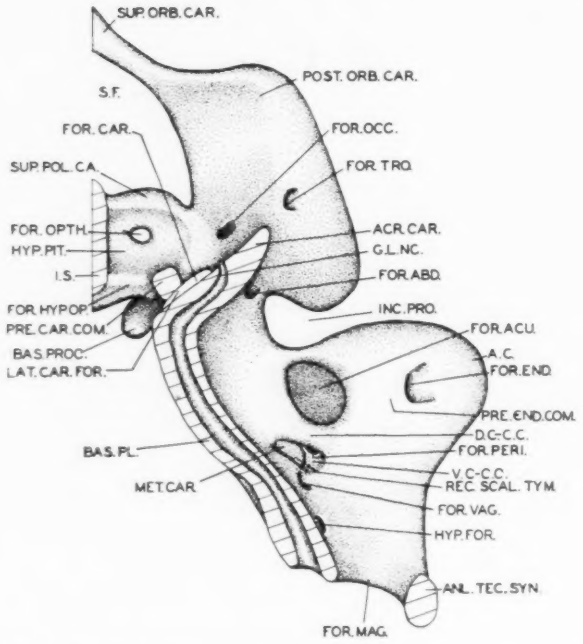


Fig. 21 (X ± 10.6). Stage 5. Disposition of cranial entities as viewed from a median sagittal section.

2. *The Orbital Region*

The most marked development of the interorbital septum in this stage is immediately in front of the hypophysial region. The anterior ends of the suprapolar cartilages have fused with the latero-posterior surfaces of the interorbital septum. All that now remains to indicate the original independence of the suprapolar cartilages are the large ophthalmic foramina. A deep hypophysial pit (*HYP. PIT.*, figs. 19, 21) bordered posteriorly by the acrochordal plate, anteriorly by the posterior edge of the interorbital septum, laterally by the suprapolar cartilages, and ventrally, incompletely, by the precarotid commissure, lodges the hypophysis cerebi. Two median foramina, the foramen caroticum and the foramen hypophyseos open ventrally into this pit.

The dorso-medial region of the basitrabecular process is fused to the antero-ventral surface of the polar cartilage. The medial region of the basitrabecular process is extended slightly medially so as to lie directly beneath the precarotid commissure. Simultaneously, the base of the acrochordal plate has migrated forwards, so that syndesmotic continuity is established between the lateral regions of the acrochordal plate and the ventro-medial regions of the basitrabecular processes. The result is that the lateral carotid incisure is transformed to a lateral

VOL. 34 1953

carotid foramen (*LAT. CAR. FOR.*, figs. 18, 21). This foramen, through which the carotid artery of the same side passes in order to reach the median foramen caroticum, is bordered dorsally by the polar cartilages, ventrally by the lower end of the acrochordal plate, posteriorly by the fusion between the acrochordal plate and the polar cartilage, and anteriorly by the medial region of the basitrabecular process. It is of particular importance to note that the lateral carotid foramen is formed without the intervention of an infrapolar process, a characteristic typical of most avian chondrocrania.

Between the basitrabecular processes of either side, the precarotid commissure dorsally, and the acrochordal plate ventrally, remains a small basicranial foramen (*B. C. F.*, fig. 19), opening forwards. This foramen cannot be considered homologous with the posterior basicranial foramen as it lies anterior to the acrochordal plate. However, it will be seen that in later stages the foramen occupies a position simulating the posterior basicranial foramen of other forms.

Together with the formation of the lateral carotid foramen, a narrow cavum is enclosed between the acrochordal plate and the polar cartilage. Four foramina open into this cavum: the two lateral carotid foramina, the basicranial foramen and the foramen caroticum. The connexion between Rathke's pouch and the stomadaeum has now atrophied completely, with the result that only a very small foramen hypophyseos remains.

3. *The Ethmoidal Region*

The side-wall of the nasal capsule (*N. C. S. W.*, fig. 18) makes its appearance in this stage as a simple procartilaginous plate, lying lateral to the nasal sac, which grows downwards from the edge of the parietotectal cartilage. In the ontogeny of the duck, De Beer and Barrington (1934) describe two independent cartilaginous centres for the side-wall of the nasal capsule, the paranasal cartilage and the planum antorbitale. Such independent anlages were not observed in the penguin, neither did Brock (1937) observe them in the ostrich. A small transverse plate, the planum antorbitale (*PL. ANT.*, figs. 18, 22) develops out of the lower posterior region of the capsular side-wall and forms an incomplete posterior wall to the capsule.

The ramus medialis nasi enters the nasal cavity by passing in an anteromedial direction over the dorsal edge of the planum antorbitale. A broad vertical plate of cartilage arises from the dorsal edge of the planum antorbitale postero-medially to the ramus lateralis nasi and fuses dorsally with the spheneth-moid commissure to enclose the ramus medialis nasi in its own foramen. No mention is made of this commissure in the literature, and for this reason the term postprofundal commissure (*POST. PROF. COM.*, fig. 22) is introduced in this paper. The profundus foramen is bordered dorsally by the parietotectal cartilage, anteriorly by the posterior edge of the side-wall of the nasal capsule,

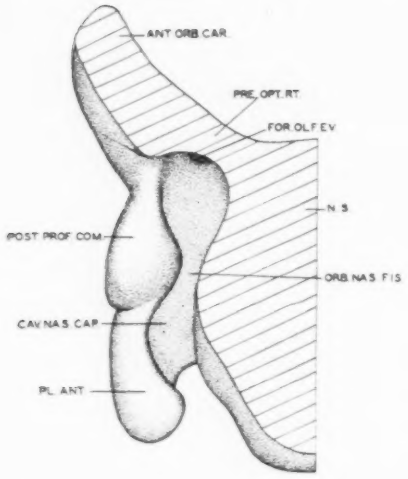


Fig. 22 (X ± 33.3). Stage 5. Reconstruction of a portion of the hinder region of the nasal capsule.

VOL. 34 1953

ventrally by the dorsal edge of the planum antorbitale and posteriorly by the postprofundal commissure. Although this latter postprofundal commissure develops out of the planum antorbitale, it cannot be considered as homologous with the latter structure, as it lies medial to the ramus medialis nasi.

The cavity of the nasal capsule is confluent with the orbit behind on account of the presence of the orbitonasal fissure (*ORB. NAS. FIS.*, fig. 22) which is bordered dorsally by the sphenethmoid commissure, medially by the nasal septum and laterally by the postprofundal commissure and the medial edge of the planum antorbitale.

4. *The Visceral Arches*

A shallow groove which lodges the posterior end of the quadratojugal ossification has now developed on the lateral surface of the antero-ventral region of the pars quadrata.

Meckel's cartilage has further increased in length to keep pace with the forward growth of the prenasal process.

In the previous stage it was seen that the anlage of the processus infracolumellaris had fused with the epihyal. Although the present stage is considerably older than the 51 mm stage, it is still possible to observe the processus infracolumellaris as a separate entity. It is separated from the epihyal by means of a narrow connective tissue disc. A broad band of dense connective tissue still connects the stylohyal with the columella auris.

F. STAGE VI

(Figs. 23 to 26.)

Total length of embryo: 61 mm.

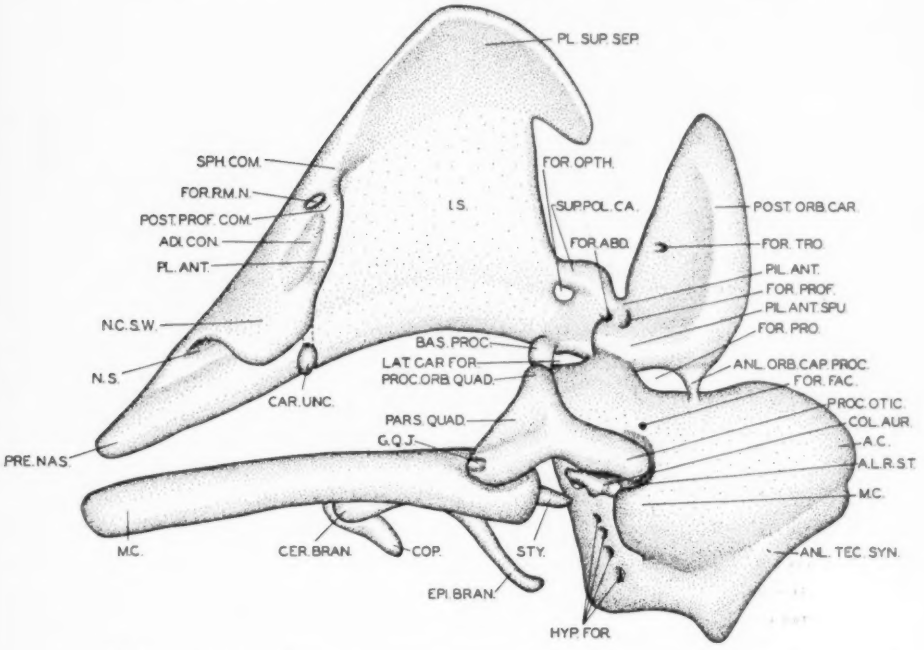


Fig. 23 (X ± 13.8). Stage 6. Reconstruction of the chondrocranium (norma lateralis).

1. *The Basal Plate and Auditory Capsule*

The narrow blastematous tectum synoticum of earlier stages has developed further to form a broad band of tissue, connecting the posterior regions of the auditory capsules.

The posterior orbital cartilages are further reduced in thickness to form a thin, transversely disposed concave plate. Together with the further extention of the posterior orbital cartilage dorsally and laterally, there is an accompaning degeneration of the medial region of this cartilage. As a result the trochlear nerve passes through the cartilage near to its medial edge.

A narrow strip of early procartilaginous tissue, the anlage of the orbitocapsular process (*ANL. ORB. CAP. PROC.*, fig. 23), stretches from the ventro-lateral edge of the posterior orbital cartilage to the dorsal surface of the auditory capsule. With the development of this process, the incisura prootica is transformed into a foramen prooticum (*FOR. PRO.*, fig. 23), bordered anteriorly by the pila antotica spuria, dorsally by the ventral edge of the posterior orbital cartilage, ventrally by the dorsal surface of the auditory capsule and posteriorly by the anlage of the orbitocapsular process. In the duck, De Beer and Barrington (1934) were able to distinguish in this region two independent processes which grew towards each other and fused to form the posterior

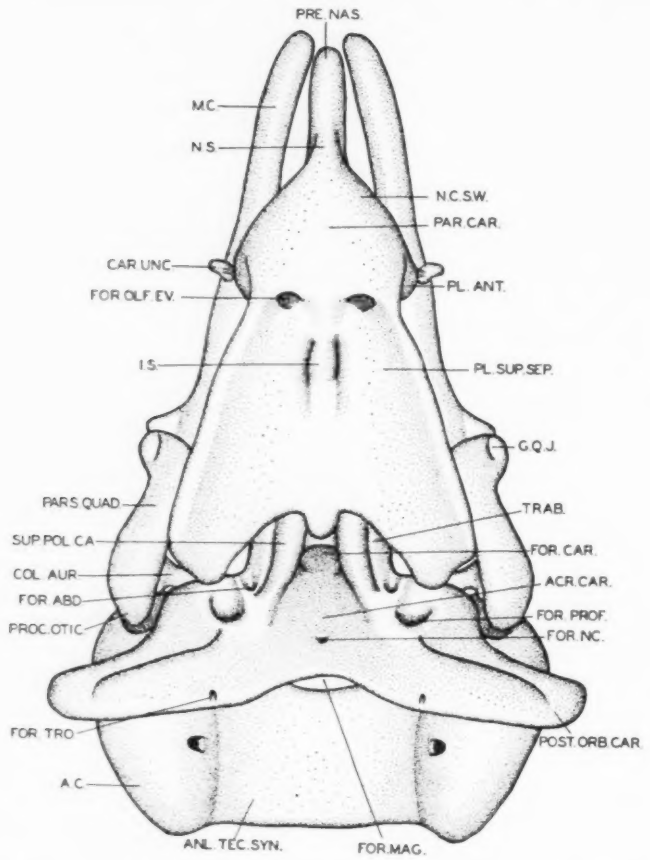


Fig. 24 (X ± 13.8). Stage 6. Reconstruction of chondrocranium (norma dorsalis).

border of the foramen prooticum. They are: (1) the orbitocapsular process from the orbital cartilage and (2) the prootic process from the auditory capsule. As a clear demarcation may be drawn between the anlage of the orbitocapsular process and the dorsal surface of the auditory capsule, there is no reason to assume that a prootic process is present in the penguin.

The anterior wall of the oculomotor canal has completely atrophied with the result that the nerve passes downwards to the eye-muscles in a shallow groove in the anterior surface of the region of the pila antotica and of the posterior orbital cartilage.

Narrow strips of atrophied cartilaginous tissue still connect the proximal region of the pharyngohyal with the pars canalicularis. The facial nerve canal is now fully formed, and in consequence, the facial finally passes outwards without traversing the cavity of the auditory capsule.

VOL. 34 1953

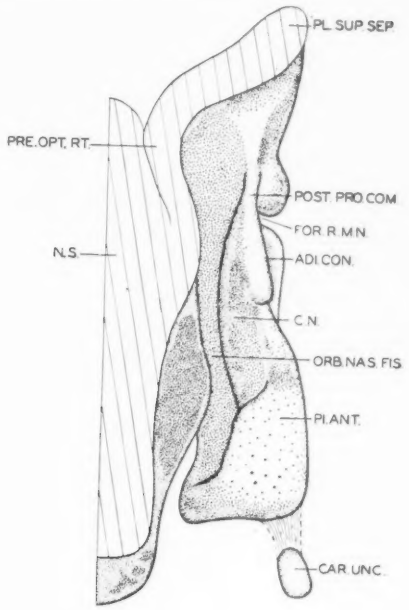


Fig. 25 (X ± 27.3). Stage 6. Reconstruction of a portion of the hinder region of the nasal capsule.

2. *The Orbital Region*

Owing to the large size of the eyes, the slender connexion between the two regions of the orbital cartilage has atrophied.

The lower lateral regions of the acrochordal plate have fused to the ventromedial portions of the basitrabecular processes. The anlage of the pterygoid bone, which lies near to the distal termination of the basitrabecular process, has now appeared. As a result, the blastematous connexion between the pars quadrata and the processus basitrabecularis has broken down.

A marked developmental feature of this stage is the dorsal growth of the interorbital septum. The posterior regions of the anterior orbital cartilages seen in previous stages as two plates of cartilage lying alongside the interorbital septum, have migrated medially. Their ventral halves are cemented to the dorsal region of the interorbital septum (fig. 25), while their dorsal halves extend laterally to form a horizontal plate, the planum supraseptale (*PL. SUP. SEP.*, figs. 23, 24, 25). Consequently the anterior orbital cartilage seen in transverse section is L-shaped. A remnant of the former connexion between the two regions of the orbital cartilage appears as a short blunt process directed backwards from the planum supraseptale towards the posterior orbital cartilage.

3. *The Ethmoidal Region*

Considerable progress may be observed in the nasal capsule of this stage. However, the anterior portion is as yet poorly chondrified. The side-wall of the nasal capsule has increased in length, mainly by addition to its anterior region. As a result of the increased height of the posterior region of the nasal septum, the postprofundal commissure has been lengthened to form a long vertical plate, lying practically parallel to the nasal septum. Ventrally the postprofundal commissure passes into the planum antorbitale with a gentle curve. Owing to the excessive development of the postprofundal commissure, the planum antorbitale remains rudimentary and forms an incomplete posterior wall to the nasal capsule. The postero-ventral edge of the side-wall is turned inwards to form a rudimentary floor (*RUD. FLOOR.*, fig. 29) to the nasal capsule (solum nasi).

The concha nasalis has made its appearance in this stage. It is formed by a folding of the nasal capsule side-wall into the cavity of the nasal capsule in a medial and slightly forward direction. Consequently, the "turbinal" of the concha nasalis develops in the penguin as a simple folding of the side-wall of the capsule. A wide aditus of the concha nasalis (*ADI. CON.*, figs. 23, 25) opens postero-laterally. The concha nasalis stretches from the postero-dorsal region of the nasal capsule downwards and sligthly forwards. The dorsal end of the concha nasalis lies in the postprofundal commissure behind the profundus foramen, with the result that, together with the formation of the concha nasalis, the profundus foramen is displaced sideways so that it now opens not laterally, but latero-posteriorly.

Ventral to the posterior edge of the nasal capsule a small independent nodule of cartilage, the cartilago uncinata (*CAR. UNC.*, figs. 23, 25) is found. Although it is difficult to be positive, the nodule appears to chondrify in the anterior remnant of the pars pterygoidea. The cartilago uncinata is connected to the ventral edge of the planum antorbitale by means of a short ligament.

4. *The Visceral Arches*

The independent anlage of the processus infracolumellaris seen in the previous stage has now fused with the medial region of the epihyal. Only a slender tract of blastematous tissue remains between the stylohyal and the columella auris.

The branchial arch is now completely chondrified. A diathrosis has developed between the ceratobranchial and the epibranchial, and between the ceratohyal and the copula. The posterior ends of the epibranchials are flexed laterally.

A short blastematous process, the remnant of the processus lingualis, stretches forwards from the anterior end of the copula. A narrow blastematous plate,

VOL. 34 1953

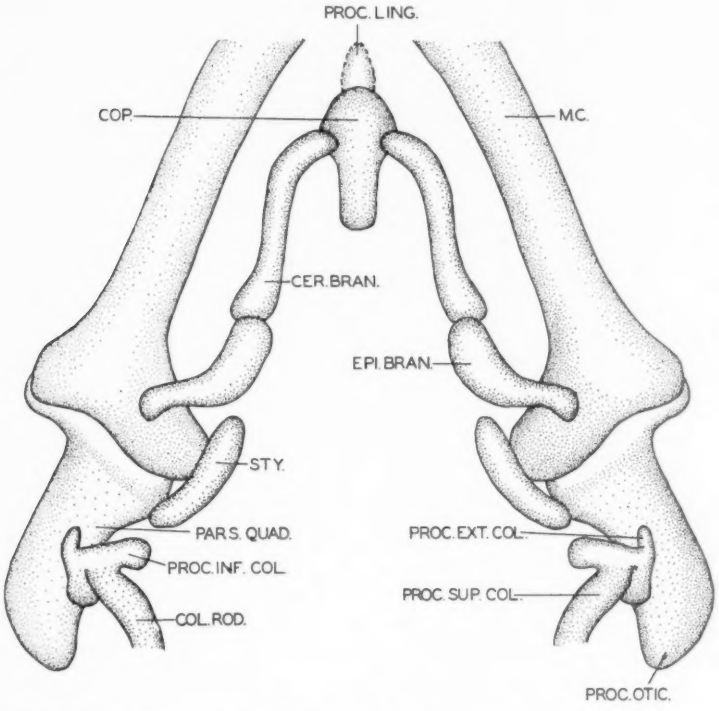


Fig. 26 (X ± 23.6). Stage 6. Reconstruction of the visceral arches (norma ventralis).

the anlage of the paraglossal cartilage, is situated dorsally to the anterior region of the copula. On either side of this plate a centre of condensation of the tissue is observable. These indicate the paired nature of the paraglossal cartilage. Anteriorly the anlage of the paraglossal cartilage merges into the blasteme of the entoglossal process.

G. STAGE VII

(Figs. 27 to 30.)

Total length of embryo: 74 mm.

The main characteristic of this stage is the straightening out of the cranial flexure.

1. *Basal Plate and Auditory Capsule*

All that now remains of the medial region of the acrochordal plate is a narrow strip of disentegrated cartilage which does not completely surround the notochord. Ventrally the anterior surface of the notochord (*N. C.*, fig. 27 c) tra-

verses the posterior region of the basicranial foramen. The reduction of the dorsal region of the acrochordal plate is indicated by the proximity of the foramen, through which the anterior tip of the notochord projects, to the dorsal surface of the acrochordal plate. In earlier stages the acrochordal plate was continued for a considerable distance, dorsally, above the notochord foramen.

Further reduction of the medial region of the posterior orbital cartilage has freed the trochlear nerve. As a result of this reduction, the medial edge of the posterior orbital cartilage presents a serrated contour.

Owing to the disentegration of the cartilage previously forming the groove for the oculomotor nerve, the nerve now passes forwards, out of the cranial cavity, dorsal to the surrounding cartilaginous structures.

The large acustic foramen observed in earlier stages has been subdivided into four small foramina. However, the extent of the original large foramen is indicated by a shallow depression (*CA. L. G. G.*, fig. 27 c) lodging the geniculate ganglion. The internal foramen of the facial nerve canal opens into the anterior region of this depression. In this stage the cartilage of the pars canalicularis surrounding the proximal region of the pharyngokyal has atrophied completely, so that a small foramen ovale is formed. It is probable that part of the pars canalicularis, to which the pharyngohyal was fused, contributes to the formation of the foot plate of the columella auris.

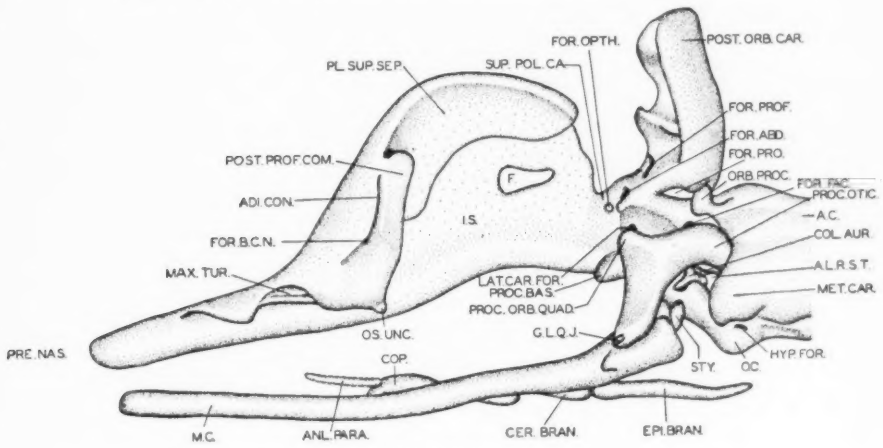
Postero-ventrally, where the metotic cartilage is fused to the lateral region of the auditory capsule, resorbtion of cartilage has been responsible for a short canal which connects the cavum metoticum with the exterior. The free anterior end of the metotic cartilage has grown further forward. The anlage of the orbitocapsular process has chondrified (*ORB. PROC.*, fig. 27) and fused to the lateral surface of the auditory capsule, dorsal to the articulatory facet of the processus oticus.

VOL. 34 1953

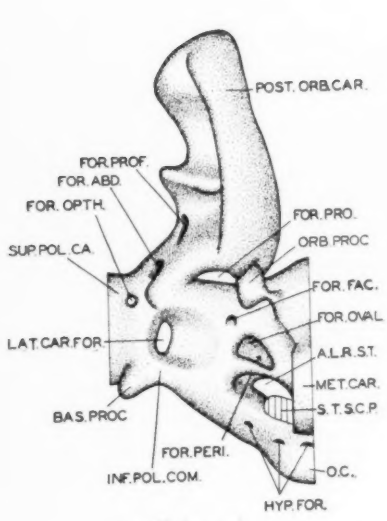
2. The Orbital Region

As a result of the straightening out of the cranial flexure, the posterior edge of the trabeculae, the medial region of the basitrabecular process, and the lower lateral regions of the acrochordal plate have been stretched to form a broad infrapolar commissure (*INF. POL. COM.*, fig. 27 b) which serves as a ventral border to the lateral carotid foramen. This simulates the infrapolar process of other avian chondrocrania. However, it was shown in previous stages that no infrapolar process, strictly homologous with the infrapolar process of other birds, is found in the penguin. As a further result of the straightening out of the cranial flexure, the basicranial foramen comes to lie vertically below the medial foramen caroticum and opens downward, and not forwards, as in the previous stage.

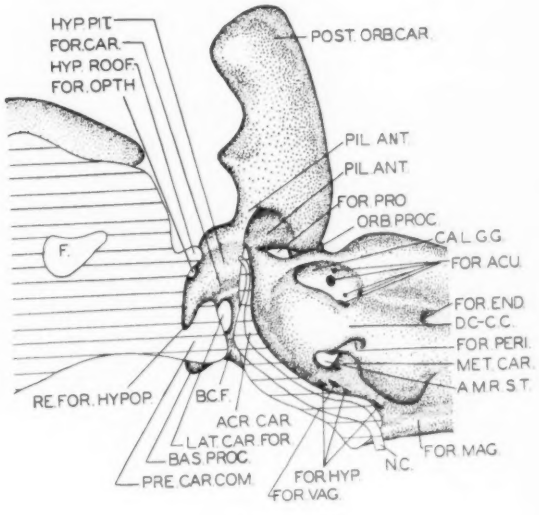
Fusion of the trabecular bars with each other in the midline, and with the



A. (X ± 8.3).



B. (X ± 13.3).



C. (X ± 13.3).

Fig. 27. Stage 7.

A. Reconstruction of chondrocranium (norma lateralis).

B. Reconstruction of the hypophysial region (norma lateralis). Pars quadrata and metotic cartilage have been removed.

C. Median view of the posterior region of the auditory capsule.

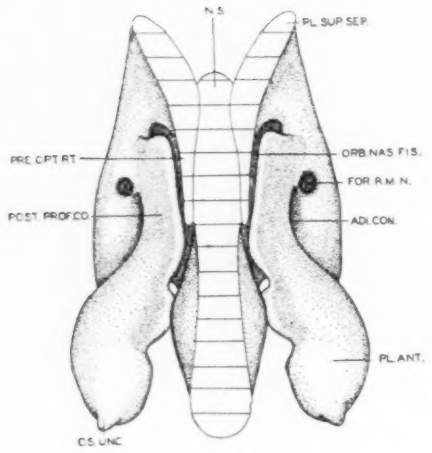


Fig. 28 (X ± 11.0). Stage 7. Reconstruction of the nasal capsule (norma posterior).

precarotid commissure behind, now occludes the hypophysial foramen. In a sagittal section the dorsal remnant (*RE. FOR. HYPOP.*, fig. 27 c) of this foramen may be observed as a narrow cavum lying anterior to the dorsal region of the precarotid commissure.

The region of the supratrabecular cartilage lying dorsal to the ophthalmic foramen, has begun to atrophy. A short horizontal roof (*HYP. ROOF.*, fig. 27 c) overlying the anterior region of the hypophysial pit, has developed from the posterior surface of the interorbital septum. The optic chiasma lies immediately above this roof. The optic nerves are lodged in a shallow notch in the posterior region of the interorbital septum.

The basitrabecular process, which now articulates with the pterygoid, extends laterally and slightly forwards.

A large fontanelle (*F.*, fig. 27 a, b) has developed in the posterior region of the interorbital septum. The planum supraseptale has undergone reduction and now remains as a narrow horizontal plate. However, it may still be distinguished from the interorbital septum as a separate entity (fig. 27 a).

3. *The Nasal Capsule*

The anterior region of the nasal capsule is still in an early state of chondrification. A very long prenasal process stretches beyond the anterior limit of the nasal capsule.

A small oval fenestra septi nasi posterior (*F. S. N. P.*, fig. 34) has made its appearance in the nasal septum. In a sagittal section of the latter the anterior region of the nasal septum is low, while posterior to the fenestra septi nasi posterior it rises rapidly to attain a height equal to that of the interorbital

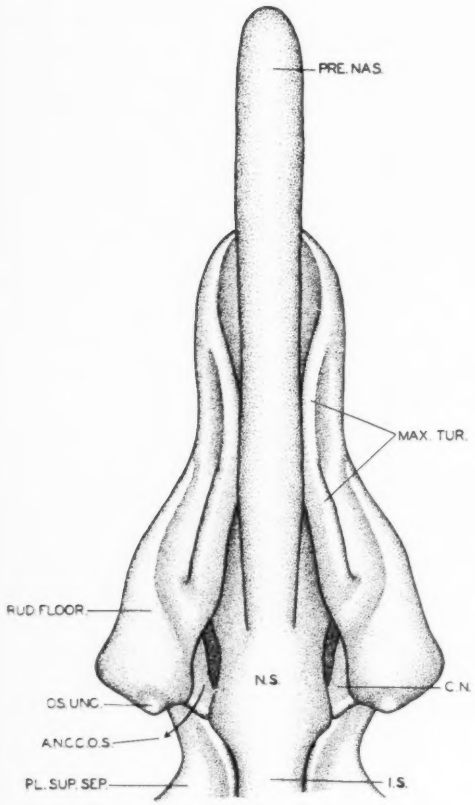


Fig. 29 (X ± 16.6). Stage 7. Reconstruction of the nasal capsule (norma ventralis).

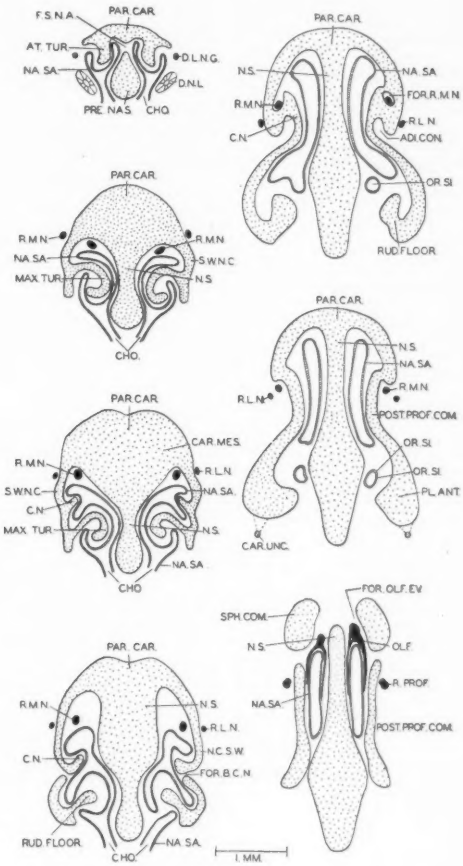


Fig. 30. Stage 7. Series of transverse sections through the nasal capsule.

septum. The dorsal region of the septum immediately behind the fenestra septi nasi posterior is triangular in shape. It is in this large cartilage mass that the mesethmoid ossification arises. Posterior to the mesethmoid cartilage (*CAR. MES.*, fig. 30) the septum nasi narrows to merge into the interorbital septum. Ventral to the mesethmoid cartilage, a small area of the septum has begun to atrophy. This is the first indication of the craniofacial foramen.

The postprofundal commissure has grown backwards to form a broad plate, the posterior edge of which closely approaches the nasal septum, with the result that the orbitonasal fissure is narrowed down considerably. The fissure may be divided into two regions: a narrow dorsal, and a broad ventral region. The latter allowing for the passage of the orbital sinus from the nasal cavity (*A. N. C. C. O. S.*, fig. 29), is bordered incompletely: dorsally by the ventral

edge of the postprofundal commissure, medially by the nasal septum, and laterally by the medial edge of the planum antorbitale.

As a result of the further deepening of the concha nasalis, the foramen for the ramus medialis nasi now opens directly backwards. Ventrally the aditus conchae is obliterated, because the side walls of the concha nasalis fuse with one another to form a solid turbinal. Dorsally, however, the concha nasalis still has the form of a simple fold of the side wall. A narrow fissure in the side wall of the nasal capsule is found directly behind the turbinal of the solid concha nasalis (*FOR. B. C. N.*, fig. 30).

The maxilloturbinals have made their appearance in this stage. They appear as two long cartilage plates which grow inwards and downwards from the side wall of the nasal capsule. Anteriorly they arise from the ventral edge of the side wall, while posteriorly they are covered laterally by the lower region of the side wall. Posteriorly the maxilloturbinals form a rudimentary floor to the nasal capsule. In order to elucidate the anatomy of the nasal capsule, a series of transverse sections through the capsule is given in fig. 30.

The independent cartilago uncinata found ventrally to the planum antorbitale in the 61 mm stage has now ossified. The os uncinatum is embedded in the ventral edge of the planum antorbitale.

4. *The Visceral Arches*

All three processes of the columella auris: the processus supracolumellaris lateralis, the processus infracolumellaris and the processus extracolumellaris lie in the same plane and are embedded in the tympanic membrane. The connexion between the columella auris and the stylohyal has atrophied.

The first branchial arches have increased considerably in length so that their posterior regions now lie at a point level with the foramen magnum. A small pharyngobranchial is still present.

The paraglossal cartilage has developed further, but is still in an early state of chondrification. Its anterior end is directed forwards as a sharp process lying in the tongue, while its postero-ventral end articulates with the antero-dorsal surface of the copula. A small medial foramen in the posterior region of the paraglossal cartilage still indicates its paired nature.

H. STAGE VIII

(Figs. 31 to 34.)

Total length of embryo: 91 mm.

1. *The Basal Plate and the Auditory Capsule*

The medial region of the acrochordal plate has now completely atrophied. As a result, the notochord projects upwards from a small medial foramen

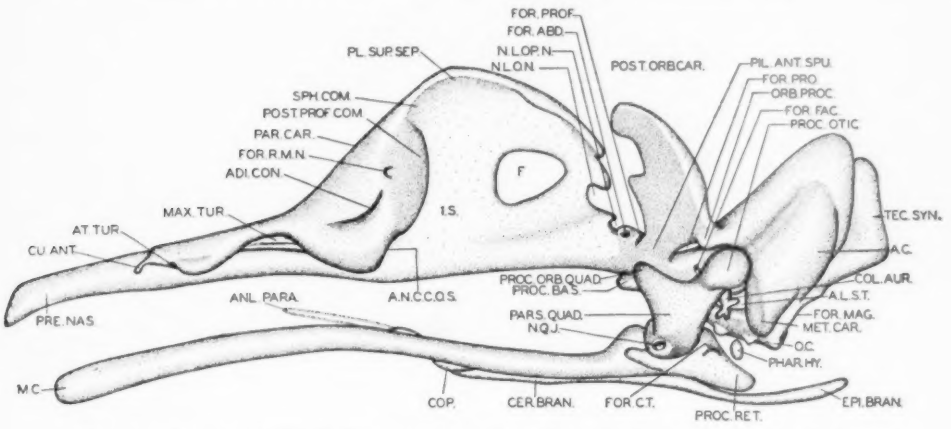


Fig. 31 (X ± 7). Stage 8. Reconstruction of chondrocranium (norma lateralis).

VOL. 34 1953

(*FOR. N. C.*, figs. 32, 33) in the antero-dorsal surface of the basal plate. Whereas in earlier stages the anterior region of the notochord was surrounded by the acrochordal plate, it is now embedded in a thick membrane (*MEM.*, fig. 33), the remnant of the acrochordal plate. In the nestling, a bony lamella, forming the posterior wall to the hypophysial pit, develops in this membrane.

Atrophy of the acrochordal plate was described by T. J. PARKER (1892 a) in *Apteryx:* "the medial portion of the dorsum sellae is formed of connective tissue in which the upturned end of the notochord is embedded." SONIES (1907) described the degeneration of the acrochordal plate till only a narrow bridge remains, forming the anterior border to the fenestra basicranialis. In the sparrow and the starling, according to SONIES (1907), the acrochordal atrophies completely, with the result that the fenestra basicranialis posterior and the fenestra hypophyseos become confluent. SONIES claims that no atrophy of the acrochordal plate is found in the fowl. However, TONKOFF (1900) showed that part of the medial wall actually does atrophy, although not as extensively as in the duck.

Only two hypoglossal foramina now remain in the basal plate. A reconstruction of the posterior orbital region shows a slender pila antotica and an extremely well-developed, broad pila antotica spuria. In the adult skull the pila antotica ossifies to form a slender pleurosphenoid lying medial to the ramus profundus.

The tectum synoticum is fully chondrified in this stage. It consists of a broad plate of cartilage connecting the ventro-posterior edges of the auditory capsule. Posteriorly it projects backwards as a short cylinder between the posterior regions of the auditory capsule.

In the latter the foramen perilymphaticum and the recessus scalae tympani have increased considerably in size. A narrow slit-like foramen places the tympanic cavity and the cavum metoticum in communication with each other. Projecting into the cavum metoticum is a short diverticulum of the middle

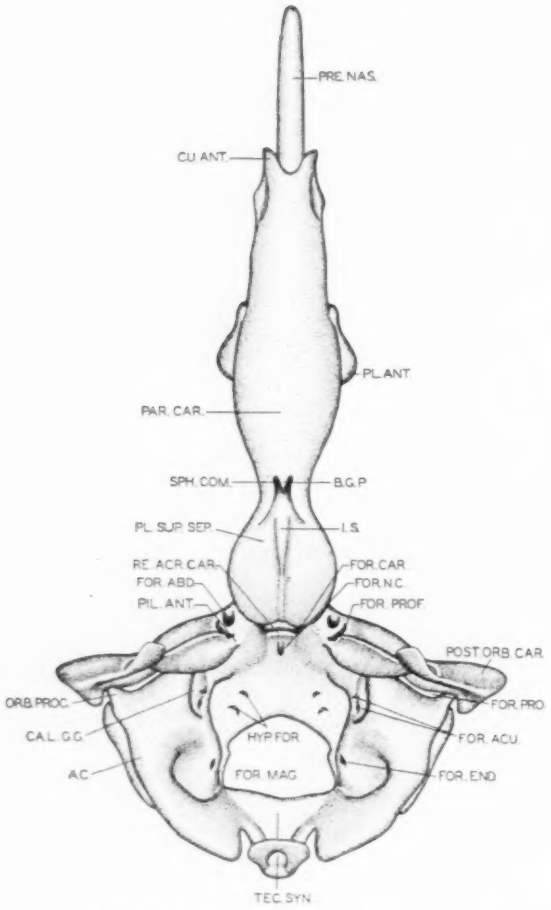


Fig. 32 (X ± 7). Stage 8. Reconstruction of chondrocranium (norma dorsalis).

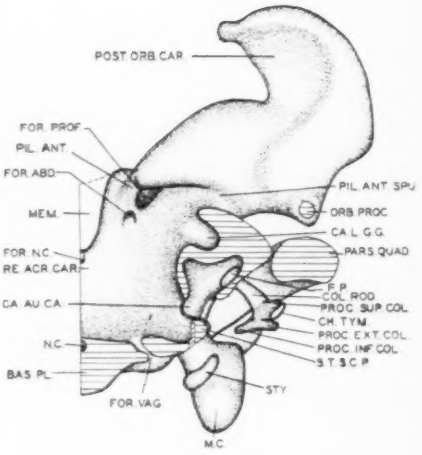


Fig. 33 (X ± 9). Stage 8. Auditory region of the skull.

ear. The rest of the cavum is filled with loose connective tissue. In the adult skull, however, the diverticulum completely fills the cavum.

The columellar rod is directed outwards and downwards so that a fairly sharp flexure occurs.

2. *The Orbital Region*

In contrast to the previous stage the hypophysial foramen is still open. Fusion of the infrapolar commissures of either side with each other in the midline, has closed up the basicranial foramen. On the right side the suprapolar cartilage remains as a slender cartilage bridge above the ophthalmic artery, but on the

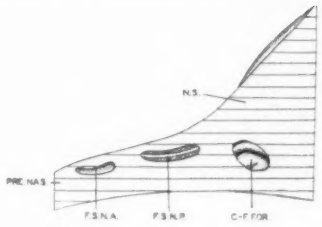


Fig. 34 (X ± 14). Stage 8. Disposition of the foramina of nasal septum.

left it has atrophied, with the result that the ophthalmic artery is lodged in a deep notch. The groove lodging the optic arteries has deepened considerably.

Two small processes projecting forward from the skull base are all that remain of the once extensive basitrabecular processes. It has been shown in an earlier work (CROMPTON, in press) that these processes ossify later. However, when the joint between the pterygopalatine arcade and the parasphenoid becomes functional late in ontogeny, the ossified basitrabecular processes atrophy into thick ligaments stretching from the skull base to the pterygoid.

The fontanelle in the interorbital septum is now larger. During the further development of the skull, the size of this fontanelle continues to increase until only the small anterior region of the interorbital septum persists in the adult skull. Further reduction of the planum supraseptale is observable in this stage.

3. *The Nasal Capsule*

Three foramina are now found in the nasal septum, the fenestra septi nasi anterior (*F. S. N .A.*, fig. 34), the fenestra septi nasi posterior (*F. S. N. P.*, fig. 34) and the craniofacial foramen (*C-F. FOR.*, fig. 34).

The postprofundal commissure has extended its area of fusion with the sphenethmoid commissure above and has fused with the nasal septum behind, to obliterate the dorsal region of the orbitonasal fissure. A broad ventral fissure remains for the passage of the orbital sinus. The fusion of the side walls of the concha nasalis has spread dorsally. A long fissure in the side wall of the nasal capsule, co-extensive with the concha nasalis, is found immediately behind the turbinal.

In the duck the maxilloturbinal gyrates up to 1 ½ times. In contrast to this, the maximum gyration found in the penguin is ¾ of a turn. The anterior region of the side wall is fully formed. Stretching downwards from the dorsal surface of the anterior parietotectal cartilage is a long cartilaginous curtain, the atrioturbinal (*AT. TUR.*, fig. 31). Its posterior end overlaps the anterior edge of the maxilloturbinal. An anterior wall to the fenestra narina, the cupola anterior (*CUP. ANT.*, fig. 31), has developed from the anterior parietotectal cartilage. In the duck (DE BEER and BARRINGTON, 1934) and the kestrel (SUSHKIN, 1899) the lamina transversalis stretching from the cupola

VOL. 34 1953

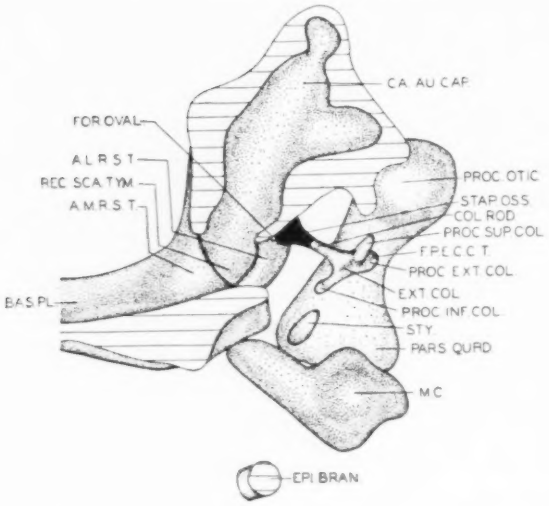


Fig. 35 (X ± 7). Stage 9. Columella auris viewed from behind.

anterior to the median septum forms a floor to the anterior region of the nasal capsule. No such structure is found in the penguin.

I. STAGE IX

(Figs. 35 to 36.)

Total length of embryo: 150 mm.

No complete description of the chondrocranium will be given for this stage.

In the columella auris of the right side, a slender bar of cartilage stretches between the lateral surface of the p. supracolumellaris lateralis and the dorsal surface of the p. extracolumellaris, to form the lateral border of a small foramen traversed by the chorda tympani. This cartilage bar must not be confused with the laterohyal, (see later section) as it lies lateral and not medial to the chorda tympani. The flexure of the columella auris has straightened out. As the medial portion of the rod, including the foot plate, has ossified to form the stapes, it is now possible to divide the columella auris into two portions, an ossified stapedial and a cartilaginous extracolumellar. The columella auris chondrified as a single structure before ossification set in, so it is impossible to ascertain whether the two divisions of the columella auris are co-extensive with the pharyngohyal and the epihyal. No joint develops between the stapes and the extracolumella. A small stylohyal persists ventral to the p. infracolumellaris.

In the nasal capsule the three foramina have increased considerably in size

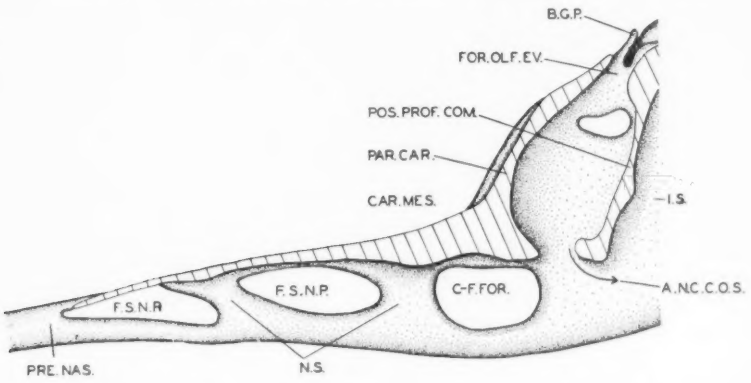


Fig. 36 (X ± 7). Stage 9. Reconstruction of median view of nasal capsule.

so that little of the original nasal septum remains. Below the foramen olfactorium evehens an additional foramen has appeared in the nasal septum.

In the nestling penguin the mesethmoid cartilage ossifies and the entire anterior region of the nasal capsule remains cartilaginous throughout life. Within the postprofundal commissure and the planum antorbitale the second ossification of the nasal capsule, the ectethmoid, develops. This latter bone is synostotically joined to the mesethmoid medially and dorsally. The membrane bones of the beak are syndesmotically connected to the anterior region of the nasal capsule and the prenasal process. As a result of the above attachment, common to adromoeognatic birds, the anterior region of the nasal capsule together with the membrane bones of the beak shift upwards during kinesis. In order that this may take place in the penguin, the ventral border of the craniofacial foramen atrophies, thus transforming the foramen into a craniofacial fissure which lies vertically below the mesokinetic line of flexure, situated between the mesethmoid posteriorly and the cartilaginous nasal capsule anteriorly. A craniofacial foramen is found in all adromoeognathic birds, but its development has only been described by SWART (1946) for the duck. SWART pointed out that the craniofacial fissure develops, not from a special craniofacial foramen as in the penguin, but from the fenestra septi nasi posterior.

DE VILLIERS (1946) has shown that in the dromoeognathic birds the entire nasal septum ossifies in continuity with the orbitosphenoid. During the kinesis the dorsal membrane bones of the beak are lifted away from the dorsal edge of the ossified nasal septum.

A small process (*B. G. P.*, fig. 36) which is directed backwards arises from the posterior central edge of the parietotectal cartilage. In the fowl and the duck this process is so large that it covers the anterior part of the interorbital septum.

The aditus conchae is now completely obliterated by the fusion of the side walls of the concha nasalis with each other.

PART II

I. RÉSUMÉ AND DISCUSSION

A. COLUMELLA AURIS

1. *Development of the Columella Auris of the Penguin*

Before discussing the avian columella auris in detail, a short summary of its development in the penguin will be given.

In the first stage four blastematous anlages constitute the hyoid arch. For convenience sake the anlages are named the pharyngo-, epi-, cerato-, and hypohyal elements. These divisions are not necessarily homologous with the similarly named ones in the hyoid arch of the fish. The epi-, cerato- and hypohyal elements abutt against one another, while the pharyngohyal, which is fused to the auditory capsule, is connected to the epihyal by a strand of connective tissue. The p. supracolumellaris lateralis develops from the lateral surface of the epihyal and projects dorso-laterally past the ventro-lateral surface of the pharyngohyal. In stage II the hypohyal and the ceratohyal have fused to form a long blastematous rod. The pharyngohyal grows ventrally as a short process to form the rod of the columella auris. In stage III the pharyngo- and epihyal have chondrified and fused to form the columella auris. From the ventral region of the epihyal, the p. extracolumellaris develops. Continuous with the dorsal end of the p. supracolumellaris lateralis is a nodule of dense blasteme situated between the p. oticus and the metotic cartilage. This nodule is probably homologous with the intercalary of reptiles. An amphistylic jaw suspension is therefore represented in the early developmental stages of the penguin. However, this amphistylic condition cannot be considered homologous with the amphistylic jaw suspension of the crossopterygians, where it is found as a result of the connexion between the processus quadratus of the hyomandibular and the posterior surface of the quadrate (WESTOLL, 1943). The processus quadratus is homologous with the processus internus of reptiles, a process not found in birds. With the disappearance of the blastematous intercalary in stage III an autostylic condition is effected.

The p. infracolumellaris develops as an outgrowth of an independent chondrification developing within the ceratohyal blasteme. This ceratohyal chondrification later fuses with the epihyal. In other avian orders that have been investigated, the p. infracolumellaris represents a remnant of the proximal region

VOL. 34 1953

of the interhyal, i.e. the connexion between the hyoid cornu and the columella auris. In the penguin apparently the interhyal completely disappears without giving rise to any adult structure. VERSLUYS showed that in *Lacerta* the p. infracolumellaris represents a proximal remnant of the interhyal while in *Geckonidae* the processus develops medial to the interhyal as in the penguin.

In the crocodile, where the p. internus does not develop, the ventral end of the hyoid cornu is fused to the posterior surface of Meckel's cartilage. This connexion led PETERS (1874) and OWEN (1846) to believe that the hyoid cornu in the crocodile was homologous with the processus internus of other reptiles. They went even further and also considered the hyoid cornu of birds as homologous with the processus internus. HUXLEY (1869) named the hyoid cornu, which in *Gallus* is fused to the columella auris, the p. infrastapedialis and also considered it homologous with the p. internus. However, both the work of VERSLUYS (1903) and my own observations on the developmental history of the hyoid arch in the penguin, make it quite clear that the p. internus of PETERS and OWEN and the infrastapedial of HUXLEY, represent the ventral end of the hyoid arch.

Within the hypohyal blasteme, the large stylohyal cartilage develops. The cartilaginous continuity existing between the stylohyal and the columella auris in several birds is not found in the penguin.

In all tetrapods the columella auris develops from two centres, here named the pharyngo- and epihyal elements, but generally designated "otostapes" and "hyostapes". In some forms e.g. *Lacerta agilis* (HOFFMANN, 1889 and VERSLUYS, 1903), *Crocodilia* (GOLDBY, 1925), *Sphenodon* (WYETH, 1924), *Struthio* (BROCK, 1937), *Tinnunculus* (SUSHKIN, 1899), *Columba* (SMITH, 1905) and *Spheniscus demersus,* a continuity, either blastematous or cartilaginous, is found between the otostapes and the auditory capsule during the ontogeny. Because of this HOFFMANN (1889) named the proximal region of the columella auris the "otostapes", thereby implying that it developed from the auditory capsule, and the distal portion the "hyostapes", which he believed represented the dorsal portion of the hyoid arch. REICHERT (1837), HUXLEY (1869), VERSLUYS (1903), GOODRICH (1930) and DE BEER 1937) all, however, consider that the entire columella auris is a derivative of the hyoid arch, and this view has been supported by recent palaeontological findings. In the above-mentioned forms the cartilage of the auditory capsule to which the pharyngohyal ("Otostapes") is fused, atrophies in the later ontogeny to form the foramen ovale. It is possible, therefore, that the auditory capsule contributes to the formation of the footplate. VERSLUYS (1903) explains the continuity existing between the columella auris and the auditory capsule as the result of the blastematous anlages of both the auditory capsule and the "otostapes" arising simultaneously and developing together. In a form such as *Platydactylus,* for example, where the blastematous anlages of the auditory capsule and the otostapes do not arise

together a distinction may be drawn between the two entities, throughout the ontogeny.

The chorda tympani of the penguin follows a typical course. It passes forwards from behind the stapes; lateral to the p. supracolumellaris lateralis and dorsal to the p. extracolumellaris. BROCK (1937) described the following course for the chorda tympani in the penguin: "The chorda tympani branches from the hyomandibular immediately above the columella shaft and then passes forward in a precolumellar course towards the trigeminal ganglion." But what BROCK here describes is not the chorda tympani but probably one of the numerous sympathetic nerves found in this region.

2. *Development of the Columella Auris in the Duck*

The development of the columella auris of *Anas* was described by DE BEER and BARRINGTON (1934), but, as it was not studied in detail, an investigation of the development of this structure was undertaken.

In the 4½ day embryo the columella auris consists of two distinct procartilaginous centres lying against each other: the "otostapes" and the "hyostapes". Neither DE BEER and BARRINGTON (1934) nor SONIES (1907) observed this division. These cartilaginous centres are homologous with the blastematous anlages, epihyal and pharyngohyal, found in the penguin but, whereas the demarcation between the pharyngo- and epihyal in the penguin is lost when chondrification sets in, the distinction is retained in the duck. Proximally the "otostapes" of the duck is in a blastematous state, but may be distinguished from the blasteme of the auditory capsule. A thin tract of procartilaginous tissue, the interhyal, connects the stylohyal with the hyostapes. No independent ceratohyal chondrification is present. In DE BEER's description of the duck he claims the appearance of the stylohyal as an independent chondrification in the 8½ day embryo. SONIES (1907) also described a separate cartilaginous centre for the stylohyal. A supracolumellar arcade, the "suprastapedial arcade" of SUSHKIN (1899) consisting of dense blastematous tissue stretches from the dorso-lateral edge of the "hyostapes" to the dorso-lateral edge of the "otostapes" to enclose a small "foramen of Huxley" (*HUX. FOR.*, fig. 37). The dorsal surface of the "hyostapes" forms the ventral border to this foramen. Dorsally within this arcade a separate nodule of cartilage is present.

GOLDBY (1925) described how the p. dorsalis develops from the "otostapes" in the crocodile. VERSLUYS (1903) describes a similar development for this process in the lizards. The chondrification found in the supracolumellar arcade of the duck may possibly be homologous with the independent chondrification in the p. dorsalis of reptiles.

In the 5½ day embryo the medial region of the "otostapes" has chondrified

VOL. 34 1953

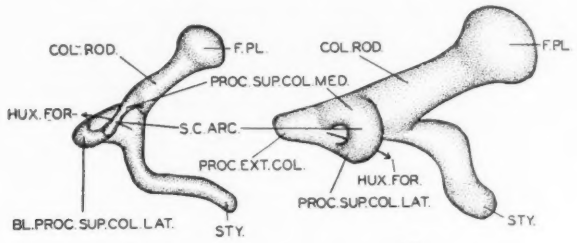


Fig. 37. The columella auris of the duck.
A. 6 ½ day embryo. B. 9 ½ day embryo.

to form a footplate and the chondrification within the supracolumellar arcade has increased in size.

In the 6 ½ day embryo (fig. 37 a) the chondrification within the supracolumellar arcade has spread medially and fused to the "otostapes". The side wall of the auditory capsule has chondrified, and a foramen ovale, lodging the footplate of the columella auris, is formed.

In the 9 ½ day embryo (fig. 37 b) the "oto-" and "hyostapes" have fused. A p. extracolumellaris develops from the lateral surface of the hyostapes. The cartilage in the supracolumellar arcade has spread laterally to fuse with the "hyostapes", so that a cartilaginous arcade "stretching" between "otostapes" and "hyostapes" is formed. The medio-dorsal region of this arcade projects dorsally as a short process. Two dorsal processes are thus found in the duck: a medial process developing from the "otostapes", homologous with the p. dorsalis in reptiles and a lateral process developing from the hyostapes, homologous with the p. supracolumellaris lateralis of the penguin. Dorsally they fuse with each other to enclose Huxley's foramen.

The relationship between the p. dorsalis of reptiles and the medial process of birds was pointed out by Huxley (1869), Versluys (1903) and De Beer (1937). Huxley (1869) named the dorsal process of reptiles and the medial process of birds the p. "suprastapedialis".

De Beer (1937) is aware of the existence of two dorsal processes and their affinities in the different groups, but uses the same nomenclature to cover both processes: "the lateral prong of the hyoid" or the "suprastapedial process". He does, however, observe that the medial process develops from the "otostapes" and the lateral process from the "hyostapes".

Stresemann (1927—34) mentions only one process in birds, the p. supracolumellaris which has to include both the medial and the lateral processes of the columella auris. Wyeth (1924) has named the lateral process in *Sphenodon* the p. suprastapedialis and the medial process the "recurrent process".

In order to avoid confusion the medial process will be named the p. supracolumellaris medialis and the lateral the p. supracolumellaris lateralis.

3. *Columella Auris of the Fowl, Kestrel, Starling, Nightjar and Ostrich.*

The development of the columella auris of the fowl was investigated by SONIES (1907). As in the penguin, he found an independent cartilaginous anlage for the p. infracolumellaris which later connects the stylohyal to the columella auris. He describes a foramen intracolumellare (Huxley's foramen), but like HUXLEY (1869) considers it to be a foramen within the p. extracolumellaris; its development is not described.

SUSHKIN (1899) investigated the development of the columella auris of the kestrel. Correctly, he homologizes the three processes of the columella auris with the three similar processes of the reptilian columella auris. SUSHKIN (1899) describes a blastematous suprastapedial arcade lodging an independent cartilaginous nodule.

He considers this nodule as representing a remnant of the operculum of fishes. However, SUSHKIN does not recognize a lateral process.

The columella auris of the starling has a well-developed p. supracolumellaris medialis. Fused to its lateral surface is the upper end of the p. supracolumellaris lateralis. An exceptionally long p. extracolumellaris is developed but there is no indication of the p. infracolumellaris. The stylohyal appears as two independent chondrifications.

The columella auris of the South African nightjar (*Nyctisyrigmus pectoralis pectoralis*) is rather similar to the columella auris of the duck. The p. supracolumellaris medialis and the p. supracolumellaris lateralis fuse dorsally to form a short process thus enclosing "Huxley's foramen". A long interhyal connects the columella auris with the stylohyal.

W. K. PARKER (1875 a) describes two suprastapedial processes in the columella auris of the woodpecker (*Picus viridis*).

BROCK (1937) accurately described the columella auris of the ostrich in which only the p. supracolumellaris medialis chondrifies. The p. supracolumellaris lateralis is found as a ligament stretching from the hyostapes to the tip of the p. supracolumellaris medialis. In a younger ostrich embryo (age unknown) a blastematous supracolumellar arcade containing an independent nodule is found. In the 16 day embryo the cartilaginous anlage has grown medially to fuse with the "otostapes" to form a cartilaginous p. supracolumellaris medialis. An analogous condition is found in the 6½ day duck columella auris but, whereas in the later development of the duck a p. supracolumellaris lateralis chondrifies, this process remains ligamentous in the ostrich.

The ostrich and the penguin thus represent opposite extremes in the avian columella auris. In the latter only the p. supracolumellaris lateralis develops, while in the ostrich only the p. supracolumellaris medialis chondrifies. In other birds both processes chondrify and fuse dorsally to enclose "Huxley's foramen". In *Lacertilia* and the ostrich, only the p. supracolumellaris medialis (p.

VOL. 34 1953

dorsalis) develops. In this respect the columella auris of the ostrich appears to be primitive, but it is equally possible that the ostrich condition is neotenic. It has already been pointed out that the adult condition of the columella auris of the ostrich is similar to an embryonic stage of the apparatus in the duck. A retention of the latter condition may possibly explain the condition in the ostrich.

4. *Comparative Anatomical Survey of the two Dorsal Processes in the Vertebrate Classes.*

Westoll (1943), Parrington (1949), Romer (1941) and Eaton (1939) all share the opinion that the p. supracolumellaris medialis (p. dorsalis) of reptiles is developed from the dorsal articulatory facet of the crossopterygian hyomandibular. The ventral facet, according to them, forms the footplate and medial portion of the columella auris in all tetrapods.

In *Anura* the columella auris develops from two centres of chondrification (the "otostapes" and "hyostapes") as in birds an reptiles. Arising from the "hyostapes" (pars externa plectri) in some *Anura*, e.g. *Rana*, is an ascending process which is directed towards the crista parotica with which it fuses. There is good reason to believe that it is homologous with the processus supracolumellaris lateralis of birds, as they both arise from the "hyostapes". De Beer (1937) employs the term laterohyal for both the p. ascendens in the *Anura* and the corresponding process in *Sphenodon* and birds. No p. supracolumellaris medialis develops from the "otostapes" (pars interna plectri) in *Anura*. It is interesting to note that Reinbach (1950) does not consider the hyostapes of *Amphibia* and *Amniota* as being homologous. According to him the p. dorsalis (p. supracolumellaris medialis) of reptiles and birds is homologous with the hyostapes of *Amphibia*.

In the *Gymnophiona* and *Urodela* the "hyostapes" does not appear to chondrify (De Beer, 1937). Westoll (1943) remarked upon the shortness of the columella auris in both these orders and suggests that the tympanic process (p. extrastapedialis) is included within the p. quadratus (p. internus) of the *Gymnophiona*. As the p. internus develops from the ostostapes and appears to be homologous in all groups in which it is found, the view of De Beer that the distal part of the columella auris (hyostapes) does not chondrify in the *Gymnophiona*, is more acceptable. In the *Urodela* Westoll (1943) considers that the tip of the stylus represents a greatly reduced p. tympanicus.

Kingsbury and Reed (1909) and Schmalhausen (1923) describe a ligament in the *Urodela* stretching dorsally from the tip of the stylus ("otostapes") to the squamosal. As the p. supracolumellaris medialis develops from the otostapes in birds and reptiles, it is probable that the ligamentum squamoso-columellare of the urodeles is homologous with this process and the dorsal arti-

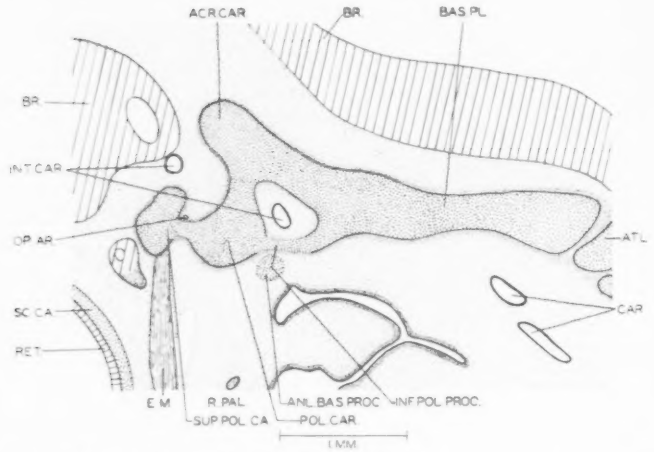


Fig. 38. Sagittal section through the infrapolar process of the emu.

VOL. 34 1953

culatory facet of the crossopterygian hyomandibular. WESTOLL (1943) does not support or refute this view. He does, however, claim a dorsal process in the typical *Stegocephalia: Eryops* and *Edops*, near the distal termination of the columella auris. ROMER points out that the stapes of the earliest amphibians is not well-known and that, although a dorsal process may be found, it is not as pronounced as it is in primitive reptiles and crossopterygians. It is not unlikely that this distal process of the *Stegocephalia* is homologous with the p. supracolumellaris lateralis (p. ascendens) found in the *Anura*, and not with the p. supracolumellaris medialis (p. dorsalis) of reptiles.

Amongst these latter a chondrified p. supracolumellaris lateralis reaching the dorsal end of the p. supracolumellaris medialis, is found only in *Sphenodon*. The dorsal ends of these processes lie between the p. oticus of the pars quadrata and the p. paroticus and are thus homologous with the intercalary found in *Lacertilia*. *Sphenodon* has no p. extracolumellaris or tympanic membrane. This led HUXLEY (1869) to believe that the foramen in the columella auris of *Sphenodon* was bordered laterally by the extracolumellaris which had rotated upwards to fuse with the p. supracolumellaris medialis. VERSLUYS (1903), however, makes it quite clear that the p. supracolumellaris lateralis (his "laterale Spange") of *Sphenodon* is homologous with the same process in birds where it is formed by the dorsal growth of the hyostapes towards the dorsal end of the p. supracolumellaris medialis. The development of the columella auris of *Sphenodon* was investigated by HOWES and SWINNERTON (1901) and WYETH (1924). None of these authors observed the division of the columella auris into "oto"- and "hyostapes". All, however, share the opinion that the suprastapedial process (p. supracolumellaris lateralis) develops from the extracolumellar cartilage.

Young developmental stages of the columella auris of *Sphenodon* are similar to those of the penguin in that only the p. supracolumellaris lateralis is developed. WYETH (1924) describes the development of a "recurrent process" (p. supracolumellaris medialis) in later stages and states, "a conspicious recurrent process is borne on the medial surface of the suprastapedial cartilage just ventral to the intercalary and extends in a ventro-medial direction almost to the dorsal surface of the medial (stapedial) extremity of the extrastapedial cartilage, to which it is firmly attached by a band of ligamentous fibres." In later stages the cartilaginous region of the recurrent process extends ventrally to fuse with the extracolumellar plate. A similar development of the medial process is described in the ostrich and the duck in this paper.

In crocodiles the p. supracolumellaris lateralis does not chondrify. Within the hyoid cornu two chondrifications commonly designated as the epi- and ceratohyals are found, which may possibly be homologous with topographically similar chonrifications found in the hyoid cornu of the penguin and which are here termed ceratohyal and hypohyal (stylohyal). During the ontogeny of the crocodile GOLDBY (1925) describes a cartilaginous continuity between the hyoid cornu (epihyal) and the columella auris. This connexion is later broken down, but a ligament stretching from the free dorsal end of the hyoid cornu to the columella auris remains to indicate the earlier connexion. A further ligament (HUXLEY and GOLDBY) is developed stretching from the epihyal (dorsal end of the hyoid cornu) to the dorsal tip of the p. supracolumellaris medialis (intercalary). A triangular foramen is thus formed, which is bordered laterally by this ligament, medially by the p. supracolumellaris medialis and ventrally by the "hyostapes" and the ligament stretching between the "hyostapes" and the "epihyal". VERSLUYS (1903) considered the ligament between the epihyal and the intercalary to be homologous with the p. supracolumellaris lateralis of *Sphenodon* and birds. The enclosed foramen would consequently be homologous with Huxley's foramen. Although this is possible, it is improbable, as the ligament arises from the free end of the hyoid cornu and not from the "hyostapes".

In lizards the conditions are obscure. According to VERSLUYS (1903) an extracolumellar ligament stretches from the insertion plate to the intercalary. Superficially this ligament appears to be homologous with the p. supracolumellaris lateralis, but BROCK (1932) gives an interpretation to this tendon which would appear to invalidate this view. VERSLUYS (1903) divides the insertion plate of the lizards into two regions. A larger pars inferior and a smaller pars superior which is represented by a small, dorsally directed process. Both these processes lie within the tympanic membrane and both develop from the hyostapes early in the ontogeny. The pars inferior appears to be homologous with the p. extracolumellaris, while it is not improbable that the pars superior represents a short p. supracolumellaris lateralis.

B. THE PARAGLOSSUM

The tongue of all birds is supported by a long slender structure, the paraglossum, which articulates posteriorly with the dorsal surface of copula 1. It may ossify completely or partially or remain cartilaginous throughout life. The anatomy of this structure in the different avian orders was admirably treated by GAUPP (1905). Many theories have been advanced over the last 110 years to explain the true nature of this structure. With the exception of KALLIUS (1905) all the authors who worked on the paraglossum considered in to be a modification of the ventral end of the hyoid cornu.

Before REICHERT, the paraglossum was called either the os linguale or the os entoglossale. REICHERT (1837) and OWEN (1846, 1866) considered that the

Nomenclature Employed for the Two Dorsal Processes of the Columella Auris in Sauropsida.

	p. supracolumellaris lateralis (penguin, author) Develops as an outgrowth of the epihyal (hyostapes)	p. supracolumellaris medialis (penguin, author) Develops as an outgrowth of the pharyngohyal (otostapes)
Penguin	present	absent
Duck, Fowl, Kestrel, Nightjar and Starling	"laterale Spange" (VERSLUYS) laterohyal (DE BEER)	p. suprastapedialis (HUXLEY) p. supracolumellaris (STRESEMANN) laterohyal or p. dorsalis (DE BEER)
Ostrich	ventrally directed tip of p. dorsalis (BROCK) ligamentous p. supracolumellaris lateralis of author (penguin)	p. dorsalis (BROCK)
Sphenodon	"laterale Spange" (VERSLUYS) p. suprastapedialis (WYETH, HOWES and SWINNERTON) laterohyal (DE BEER)	p. suprastapedialis (HUXLEY) p. dorsalis (VERSLUYS) recurrent process (WYETH)
Lizards	pars superior (VERSLUYS)	p. dorsalis (VERSLUYS) — also the term generally employed

postero-lateral aspects of the paraglossum (their glossohyal) were ceratohyals, while the anterior unpaired region was considered as homologous with the glossohyal (basihyal) of fishes.

VOL. 34 1953

W. K. PARKER (1866, 1869) claimed that the entire paraglossum was formed by the fusion of the ventral ends of the hyoid arch. However, in a later work (1891) he considered that the paraglossum also contained a basihyal. T. J. PARKER (1892) designated the paraglossum the "Y-shaped cartilage". He considered the arms of the "Y" to be ceratohyals and the medial stem a basihyal. GEGENBAUR (1898) claimed that the ventro-posterior regions of the paraglossum were formed by the hypohyals.

Up to the time of SUSHKIN (1899) the medial copula was considered a single structure. However, SUSHKIN (1899) showed that in the anlage of this structure two centres of chondrification may be observed: the copula 1 and 2. He further claimed that the paraglossum (his entoglossal) was formed by the fusion of the two ceratohyals.

KALLIUS (1905) introduced the term paraglossum and considered the bone to be a new structure in birds. GAUPP (1905) basing his argument on comparative anatomy, claimed that the paraglossal cartilage was homologous with the basihyal. SONIES (1907) and DE BEER and BARRINGTON (1934) consider the paraglossum to be formed by the fusion of the ceratohyals. DE BEER and BARRINGTON (1934) however, are prepared to accept the view of KALLIUS that the anterior copula is a basihyal.

In the youngest stage of the penguin investigated a connexion is found between the hyoid cornu and copula 1. Although this connexion has never before been described in birds, its appearance was anticipated by KALLIUS (1905). This connexion clearly indicates that the paraglossal cartilage cannot be considered a derivative of the hyoid arch as it develops in front of it, further, it indicates that copula 1 is a basihyal. Extending forwards from the anterior point of copula 1 in the early stages of the ontogeny there is a blastematous process which is probably homologous with the processus lingualis and the glossohyal of SUSHKIN (1899). However, it never chondrifies, but atrophies during the later ontogeny.

The anlage of the paraglossum appears in stage VI as a connective tissue plate lying dorsal to the anterior region of copula 1. It is probable (though this was not actually observed) that the processus lingualis contributes to the formation of the posterior region of the paraglossum.

It may be concluded, firstly, that the paraglossal cartilage in birds does not develop from the hyoid cornu, but is a de novo structure, and secondly, that copula 1 is a basihyal.

C. THE NASAL CAPSULE AND THE OS UNCINATUM

The nasal capsule of the penguin is peculiar for two reasons: firstly, the olfactory nerve enters the nasal capsule directly through the foramen olfactorium evehens, a feature found only in the *Selachii, Polypterus, Acipenser,*

Gadus, Dipnoi and *Amphibia* and secondly the ramus medialis nasi of the n. profundus enters the nasal capsule through its own foramen in the side wall of the nasal capsule.

In all forms, with the exception of those mentioned above, the foramen olfactorium evehens does not open directly into the nasal cavity, but into a extracranial space, the cavum orbitonasale. De Beer (1937) describes this condition as follows: "In some forms a relative shifting of position has taken place between the lamina orbitonasale and the preoptic root of the orbital cartilage, the former moving forward (or/and) the latter backwards. The result is that the foramen olfactorium evehens then no longer opens directly into the nasal cavity, but into a space, the cavum orbitonasale, which may be regarded as either an aquisition to the orbit or a loss to the nasal cavity." In the duck and the fowl the extensive development of the interorbital septum carries the preoptic roots dorsally, with the result that, after the olfactory nerve has passed through the foramen olfactorium evehens, it finds itself for a short distance in the orbit (cavum orbitonasale). It leaves the orbit and enters the nasal cavity through the foramen olfactorium advehens. In the further development of the duck and the fowl the orbital cartilage (planum supraseptale) separating the olfactory nerve from the orbit and lying behind the foramen olfactorium evehens, atrophies. This further increases the length of the course of the olfactory nerve through the orbit. Further there is an extensive posterior development of the parietotectal cartilage, which forms a roof to the cavum orbitonasale and the foramen olfactorium advehens. The degeneration of the orbital cartilage and sphenethmoid commissure does not take place so extensively in the penguin as to expose the olfactory nerve. The foramen olfactorium evehens is not carried dorsally as in the duck and the fowl, with the result that it opens directly into the nasal capsule. Had the preoptic roots of the penguin developed further dorsally, the conditions prevailing in the duck and the fowl would result.

In the swallow (De Beer and Barrington, 1934) as in the penguin, the orbital cartilage and the sphenethmoid commissure do not atrophy. As a result of the extensive fusion between the interorbital septum and the preoptic root in the swallow, the olfactory nerve is enclosed within a long canal which opens directly into the nasal cavity. In the ostrich (Brock, 1937) an extremely short cavum orbitonasale appears to develop.

The extensive posterior development of the parietotectal cartilage, so characteristic of the fowl, ostrich and duck, is not found in the penguin. Here the backward growth of the parietotectal cartilage is represented by an extremely short median process directed postero-dorsally from the posterior central region of the parietotectal cartilage. It only appears in the late stages of the ontogeny.

In birds and reptiles the ramus medialis nasi enters the nasal capsule through the foramen orbitonasale. This foramen is bordered dorsally by the sphenethmoid commissure, ventrally by the dorsal edge of the lamina orbitonasale, medially

by the nasal septum and laterally by the parietotectal cartilage. In the penguin, however, the ramus medialis nasi passes through a foramen in the side wall of the nasal capsule. In the early developmental stages of the nasal capsule of the penguin, the fissura orbitonasalis is divided into two: a foramen for the ramus lateralis nasi and a medial orbitonasal fissure. This is effected by means of a vertical plate of cartilage, the postprofundal commissure, which grows upwards from the dorsal edge of the planum antorbitale medially to the ramus medialis nasi and fuses with the sphenethmoid commissure. In later stages the postprofundal commissure grows obliquely backwards to form a broad plate which later fuses with the preoptic root and the nasal septum to form an oblique posterior wall to the nasal capsule. As a result of the extensive development of the postprofundal commissure, the planum antorbitale is poorly developed, forming only a rudimentary posterior wall to the nasal capsule.

OL.
34
953

In conclusion it may be said that the foramen for the ramus medialis nasi is a remnant of the originally wide, orbitonasal fissure.

In the 61 mm. stage a small independent cartilago uncinata connected to the lamina orbitonasalis by means of a thick strand at connective tissue, is found ventral to the lamina orbitonasalis. As this nodule appears to develop within the blasteme of the pars pterygoidea, it probably represents a chondrification of the anterior end of the palatoquadrate. In later stages it is found as a small ossification embedded in the ventral region of the planum antorbitale. Stretching between this ossicle and the jugal bone is a thin ligament. Towards the end of the ontogeny the ossicle atrophies, but the ligament remains to indicate its former position.

Without doubt this transitory ossification is homologous with the lacrimo-palatine ossicle or the uncinate ossicle which is found in many birds, where it extends from the ectethmoid (lateral ethmoid) to the jugal. In the penguin, however, it is smaller, and its ventral portion is represented by a ligament. PYCRAFT (1900) described a particularly well-developed uncinate ossicle in the ostrich. According to W. K. PARKER (1875 b), the os uncinatum develops from a cartilaginous bud arising from the trabeculae. DE BEER (1937) suggests that it develops from a portion of the ectethmoid that has become segmented off. GREWE (in press) describes a ligamentum lacrimo-jugale which stretches between the ventro-medial edge of the lacrimal and the jugal. He attempts to show that this ligament is preceded in the ontogeny by a cartilaginous bud which arises from the antorbital plate. Judging from the topographical position which it occupies, it appears to be homologous with the uncinate cartilage of the penguin. Although BROCK makes no mention of this structure in her description of the development of the chondrocranium of the ostrich, she indicates a similar process, directed ventrally from the lamina orbitonasalis, in the figures illustrating stage III and IV. However, as the development of the uncinate ossicle of the ostrich has not yet been described, the above suggestion is necessarily tentative.

De Beer (1937) describes a long process, the processus maxillaris posterior arising from the ventro-lateral corner of the lamina orbitonasalis. Concerning this process he says: "In many *Urodela* in *Gymnophiona, Lacertilia, Sphenodon, Chelonia, Crocodilia* and birds, the pterygoid process ends freely, but it is not impossible that the processus maxillaris posterior may represent its extreme anterior end, fused to the lamina orbitonasalis." It is possible that the uncinate ossicle of birds is homologous with the processus maxillaris posterior of Lacerta, firstly because of its topographical position and secondly because of its relationship with the blasteme of the pars pterygoidea. However, in contrast to the reptiles this structure ossifies to form the os uncinatum, whereas in reptiles it remains cartilaginous. The birds are peculiar among the *Sauropsida* in that the lamina orbitonasalis ossifies to form the ectethmoid. The lamina orbitonasalis which is homologous in all groups ossifies only in fishes and birds. In the fishes the anterior end of the palatoquadrate ossifies to form the autopalatine. This ossification is not found in the *Amphibia* or the reptiles. It is not improbable that the os uncinatum of birds is homologous with the autopalatine of fishes.

Two cartilages of flat and oval shape lying in the ventro-medial periosteum of the pterygoid, ventral to the parasphenoid, are found in an embryo of a body length of 120 mm., and have an approximate length of 0.4 mm. That they develop in situ is certain, as the connective tissue anlages of these cartilages may be seen occupying the same position relative to the pterygoid in younger stages. There are two possible explanations for these cartilages; either they represent neomorphic structures without phylogenetic importance, or they are remnants of the pars pterygoidea. As neomorphic cartilages develop in response to stress and strain the latter explanation is more probable.

D. THE BASITRABECULAR PROCESS, INFRAPOLAR PROCESS AND PRECAROTID COMMISSURE

A striking characteristic of the dromoeognathic birds is the well-developed basitrabecular process of the adult skull. In the adromoeognathic birds there is a tendency for this process to atrophy as a result of the articulation which arises between the palato-pterygoid arcade and the parasphenoidal rostrum. The basitrabecular process is found, however, in the embryos of all adromoeognathic forms. A particularly well-developed basitrabecular process is found in the ontogeny of the penguin. In the nestling this process dwindles to a ligament. This confirms the findings of Pycraft (1898, 1910) for a nestling of *Pygoceles papua*. Simpson (1946) in his description of the fossil penguin, *Pareptenodontes antiarticus* finds no indication of a basitrabecular process.

In the penguin the basitrabecular process develops from an independent anlage, which lies between the pars quadrata and the polar cartilage. In later

stages it fuses with the ventral surface of the polar cartilage. The distal region of the anlage of the basitrabecular process does not chondrify. A similarly developing basitrabecular process was described by SUSHKIN (1899) in the kestrel and by LUTZ (1942) in a 15 day old embryo of the emu. In the latter, in contrast to the penguin, the entire anlage of the processus basitrabecularis chondrifies, so that the lateral surface abuts against the pars quadrata. A large processus basitrabecularis, which reaches the pars quadrata, was observed by BROCK (1937) in the ostrich. However, no independent anlage for this process was described. In fig. 92 of T. J. PARKER's (1892 a) description of the development of the kiwi skull, an independent anlage for the basitrabecular process is indicated, but no mention is made of it in the text. In the early ontogenetic stages of the duck, DE BEER and BARRINGTON (1934) describe a band of procartilaginous tissue stretching between the polar cartilage and the pars quadrata. They consider it to be a remnant of the basal articulation. It is probable that this band is homologous with the independent anlage for the basitrabecular process found in the penguin and the emu.

VOL. 34 1953

KESTEVEN (1941, 1942) considers that the basitrabecular process of birds is not homologous with the similarly named process of the reptiles as this process develops from the polar cartilage in birds and from the trabeculae in the reptiles. For this reason he suggests the term basipolar process for the process found in birds. KESTEVEN claims that the course of the ramus palatinus in reptiles and birds offers further support to his view that the basitrabecular processes are not homologous in the two classes. According to him the main body of the ramus palatinus in birds passes forwards dorsal, to the processus basitrabecularis while only a small branch passes forwards below this process. In reptiles the characteristic position for the ramus palatinus is below the basitrabecular process. However, the division of the ramus palatinus into two branches passing forwards, one dorsal and the other ventral to the basitrabecular process, was described by ENGELBRECHT (in press) in *Microsaura pumila* and by FRANK (in press) in *Rhampholeon platyceps*. The condition of the palatine nerve, as described by KESTEVEN for the birds cannot, therefore, be considered a characteristic peculiar to the class.

In the early stages of the penguin ontogeny it is clearly seen that the ramus palatinus passes forwards below the basitrabecular process, and no branch dorsal to this process is found. In the late embryonic stages a stout sympathetic nerve accompanies the ramus palatinus forwards. Behind the basitrabecular process, the sympathetic component separates from the ramus palatinus and passes forwards dorsal to the process. In front of the basitrabecular process the greater part of the sympathetic nerve rejoins the ramus palatinus. It is probable that KESTEVEN, FRANK & ENGELBRECHT confused this sympathetic component with the true ramus profundus.

It has already been pointed out that in the penguin the processus basitra-

becularis arises from an independent anlage. It may fuse with either the trabeculae or the polar cartilage without affecting the homology of this process in different groups. If, however, the independent anlage of this process in the emu and the penguin is a secondary characteristic the process may still be considered homologous in both groups, whether it develops from the trabeculae or the polar cartilage as the polar cartilages are probably derivatives of the trabeculae.

In birds two processes, directed backwards towards the basal plate below the internal carotid arteries of either side, develop from the ventral surfaces of the polar cartilages. The posterior tips of these processes fuse with the ventral surfaces of the basal plate to form a ventral border to the lateral carotid foramen. The term infrapolar process was introduced by SONIES (1907). As SONIES could find no indication of the processus basitrabecularis in the duck or in the fowl, he considered the infrapolar process to be homologous with the basitrabecular process. LUTZ (1942) described both a basitrabecular and a basipterygoid process in the emu. The work of DE BEER (1937) and GOODRICH (1930) has shown quite conclusively that the processus basitrabecularis and the processus basipterygoideus are two names for the same structure. Serial sections of a 15 days emu embryo show that the so called processus basipterygoideus of LUTZ (1942) is homologous with the basitrabecular process anlage of the penguin and that the processus basitrabecularis of LUTZ is homologous with the infrapolar process in other forms. LUTZ apparently makes the same mistake as SONIES (1907) in considering that the infrapolar process and basitrabecular process are homologous. DE BEER and BARRINGTON (1934) make it quite clear that the processus basitrabecularis and the infrapolar process are two distinct structures.

In the penguin and the ostrich (BROCK, 1937) no definite infrapolar process developing from the polar cartilage is found. In the early stages of the penguin ontogeny a wide incisura, traversed by the lateral carotid artery of either side, is formed between the acrochordal plate and the ventral surface of the trabeculopolar bar. In the later ontogenetic stages the ventral edge of the acrochordal plate migrates forwards and fuses with the ventral portion of the basitrabecular process. As a result the lateral carotid incisure is transformed into a lateral carotid foramen without the intervention of an infrapolar process. Together with the straightening out of the cephalic flexure, the connexion between the medial region of the basitrabecular process and the acrochordal plate is stretched to form a ventral border to the lateral carotid foramen. This border simulating an infrapolar process of other birds must not be confused with a true infrapolar process.

The absence of the infrapolar process in the penguin is associated with the acute cranial flexure. Where the cranial flexure is not so large, e.g. the starling (SONIES, 1907), the fowl (SONIES, 1907, TONKOFF, 1900, BROCK, 1937), the

VOL 34 195

kiwi (T. J. PARKER, 1892 a, b) and the emu, a well-developed infrapolar process has to be formed in order to reach the basal plate below the internal carotid arteries.

The penguin is peculiar in possessing a precarotid commissure which develops from the proximal ends of the trabeculae and divides the large hypophysial foramen into two foramina. Rathke's pouch passes through the anterior foramen hypophyseos, while the internal carotid passes through the posterior foramen caroticum. Contrary to the description of LUTZ (1942) of the emu skull, faint indications of a precarotid commissure in a 15 day emu embryo were observed. However, older embryos were not available to ascertain whether this commissure actually chondrifies in the later ontogeny. A commissure similar to that of the penguin was described by T. J. PARKER (1892 a, b) in the kiwi. No precarotid commissure is found in any of the other avian chondrocrania that have been described.

In *Selachii* a precarotid commissure was described by DE BEER (1937) and ALLIS (1923). It does not, however, develop from the trabeculae as in the penguin, but from the medial surfaces of the polar cartilages. ALLIS (1923) considers the precarotid commissure of the *Selachii* as homologous with the infrapolar processus of birds. Instead of these processes fusing with each other to form a precarotid commissure as they do in the *Selachii*, ALLIS claims that they fuse with the basal plate to form the infrapolar process in birds. As no infrapolar process or precarotid commissure is found in either the reptiles or the amphibia this view is hardly tenable.

II. SUMMARY

1. No fenestra basicranialis posterior is found in the penguin.
2. Five cranial ribs are present in the early ontogeny, all however disappear during the later stages.
3. During the early ontogeny the oculomotor nerve is enclosed in a long canal situated between the pila antotica and the posterior orbital cartilage.
4. The auditory capsule arises from two centres, the pars canalicularis and the pars cochlearis.
5. The pharyngohyal ("otostapes") arises in continuity with the pars canalicularis.
6. The cartilago metotica develops as a process of the auditory capsule.
7. The basitrabecular process arises from an independent anlage lying below the polar cartilage. It is syndesmotically connected to the medial surface of the pars quadrata and lies dorso-lateral to the palatine nerve.
8. The trabeculae arise as two independent bars below the fore-brain. Their posterior ends are connected by a precarotid commissure, which later divides

the foramen basicranialis anterior into two foramina: a foramen caroticum and a foramen hypophyseos.

9. The processus orbitoquadratus chondrifies in the posterior region of the pars pterygoidea.
10. The hyoid arch develops from four independent blastematous anlages, the pharyngohyal ("otostapes"), epihyal, ("hyostapes"), ceratohyal, and hypohyal (stylohyal).
11. The processus supracolumellaris lateralis develops from the lateral surface of the epihyal.
12. The connexion in the early ontogeny between the hypohyal and copula 1, indicates that the latter is a basihyal.
13. The chorda tympani follows a typical reptilian course.
14. Copula 1 (basihyal) and copula 2 appear in the early ontogeny as two independent chondrifications. Later they fuse to form a single copula.
15. A remnant of the second branchial arch is found in the early ontogeny.
16. Throughout the greater part of the ontogeny the trochlear nerve is enclosed in a long horizontal canal within the posterior orbital cartilage.
17. The pila antotica spuria develops as a downgrowth from the posterior orbital cartilage. It fuses with the lateral abducent commissure to form the lateral border to the foramen for the ramus profundus.
18. A lateral abducent commissure stretching between the posterior orbital cartilage and the pars cochlearis, forms the lateral border to the abducent nerve.
19. The facial nerve is wedged in between the two portions of the otic capsule. In the early development the facial nerve passes through the cavity of the auditory capsule, but later it is enclosed in a cartilaginous canal.
20. The auditory foramen is the remnant of the cochleo-canalicular fissure.
21. The trabecula communis is extended forwards by a prenasal process.
22. The preoptic roots arise from the antero-lateral surfaces of the trabecula communis.
23. The interorbital septum grows upwards from the centre of the trabecula communis.
24. No intertrabecular bar is found in the penguin.
25. A transitory blastematous intercalary nodule situated between the metotic cartilage and the processus oticus appears in the early ontogeny.
26. Copula 1 is extended forwards as a blastematous process, the processus lingualis. It is possible that this process contributes to the formation of the paraglossum.
27. Up to four hypoglossal foramina appear in the left side of the basal plate during the ontogeny.
28. The nervus vagus traverses a foramen in the basal plate.
29. A supraorbital cartilage connects the two regions of the orbital cartilage.
30. The posterior regions of the auditory capsule are connected with each

VOL. 34 195

other dorsally by the dorsal cochleo-canalicular commissure and ventrally by the ventral cochleo-canalicular commissure. These commissures form the dorsal and ventral borders of the foramen perilymphaticum.

31. The nasal septum grows upwards from the posterior region of the prenasal process.
32. The sphenethmoid commissure stretching from the postero-lateral surface of the parietotectal cartilage to the posterior orbital cartilage, forms the lateral border to the foramen olfactorium evehens. No foramen olfactorium advehens is found in the penguin.
33. The processus extracolumellaris develops from the lateral surface of the hyostapes.
34. The cartilage of the pars canalicularis, to which the "otostapes" is fused, atrophies and so the foramen ovale is formed. It is possible that part of the pars canalicularis contributes to the formation of the footplate of the columella auris.
25. The processus infracolumellaris develops from the ceratohyal chondrification. It is not formed from the interhyal as in most birds and reptiles.
36. The tectum synoticum chondrifies in a broad tract of blastematous tissue connecting the posterior edges of the auditory capsules with each other.
37. A cavum metoticum is enclosed between the auditory capsule and the metotic cartilage. In the late stages of the ontogeny, a diverticulum of the tympanic cavity grows into the cavum metoticum.
38. The medial region of the cavum metoticum is extended forwards as a subcapsular process forming a floor to the recessûs scalae tympani.
39. The free anterior edge of the metotic cartilage forms a lateral wall to the apetura lateralis recessûs scalae tympani.
40. The lateral carotid foramen is formed without the intervention of an infrapolar process. This is a result of the acute cranial flexure.
41. There is a basicranial foramen simulating the foramen basicranialis posterior of other forms, but it cannot be considered homologous with the latter as it lies anterior to the acrochordal plate.
42. In the nasal capsule an independent paranasal cartilage and an antorbital plate were not observed. These two structures arise in continuity with the side wall of the nasal capsule.
43. The orbito-nasal fissure is divided into two by a postprofundal commissure. The ramus medialis nasi passes into the nasal capsule through the lateral portion of the orbitonasal fissure. In the late ontogeny the postprofundal commissure forms the major portion of posterior wall of the nasal capsule. Owing to the development of a postprofundal commissure the planum antorbitale remains rudimentary.
44. The anterior orbital cartilage fuses with the dorsal region of the interorbital septum to form the planum supraseptale.

45. The concha nasalis is formed by a simple folding of the side wall of the nasal capsule. In later stages the aditus conchae is obliterated by the side walls of the concha nasalis fusing with one another to form a solid turbinal.
46. The os uncinatum is apparently homologous with the autopalatine bone of fishes.
47. In the late ontogeny the acrochordal plate dwindles to a membrane. In the nestling this membrane ossifies.
48. Simultaneously with the degeneration of Rathke's pouch the foramen hypophyseos closes.
49. Three foramina are found in the nasal septum: a foramen septi nasi anterius, a foramen septi nasi posterius and a f. craniofaciale. The latter is transformed into a craniofacial fissure by the degeneration of the ventral border of this foramen in order that kinesis may take place.
50. The paraglossal cartilage appears to be a de novo structure found only in birds.
51. In birds, in general, and in *Sphenodon*, two dorsal processes arise from the columella auris. A processus supracolumellaris medialis develops from the otostapes and appears to be homologous with the processus dorsalis of reptiles. A processus supracolumellaris lateralis develops from the hyostapes and appears to be homologous with the processus ascendens of the *Anura*. Dorsally they fuse with each other to enclose "Huxley's foramen".
52. In the penguin only the processus supracolumellaris lateralis is present, while in the ostrich only the processus supracolumellaris medialis chondrifies.

VOL. 34 1953

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IV. ALPHABETICAL LIST OF ABBREVIATIONS USED IN THE FIGURES

ABD. Abducent nerve
AC. Auditory capsule
ACR. CAR. Acrochordal cartilage
ACU. NER. Acustic nerve
ADI. CON. Aditus concha
A.L.R.S.T. Apetura lateralis recessus scalae tympani
A.M.R.S.T. Apetura medialis recessus scalae tympani
ANL. BAS. PROC. Anlage of the basitrabecular process
ANL. C.-F. FOR. Anlage of the craniofacial foramen
ANL. ORB. CAP. PROC. Anlage of the orbitocapsular process
ANL. PARA. Anlage of the paraglossal cartilage
ANL. TEC. SYN. Anlage of the tectum synoticum
ANT. ORB. CAR. Anterior orbital cartilage
A.N.C.C.O.S. Apeture in the nasal capsule communicating with the orbital sinus
A.S. Auditory sac.
ATL. Atlas
AT. TUR. Atrioturbinal
B.C.F. Basicranial foramen
BAS. PL. Basal plate
BAS. PROC. Basitrabecular process
B.G.P. Backward growing process of the parietotectal cartilage

BL. CON. Blastematous connexion between the hyoid arch and Copula I

BL. CON. STY. Blastematous connexion between the columella auris and the stylohyal cartilage

BL. PARS. PTER. Blastematous pars pterygoidea

BL. PRO. SUP. COL. LAT. Blastematous processus supracolumellaris lateralis

BL. TR. Blastematous tract connecting the processes basitrabecularis with the pars quadrata

BR. Brain

1. BRAN. ARC. First branchial arch

2. BRAN. Arc. Second branchial arch

CA. AU. CA. Cavity of the auditory capsule

CA. L. G.G. Cavity lodging the ganglion geniculatum

CAR. Carotid artery

CAR. FLAN. Cartilaginous flange

CAR. MES. cartilage in which the mesethmoid ossification arises

CAR. UNC. Cartilage uncinata

CAV. MET. Cavum metoticum

CER. BRAN. Ceratobranchial

CER. HY. Ceratohyal

CER. HY. CHON. Ceratohyal chondrification

CER. HYP. HY. Fused ceratohyal and hypohyal blasteme

C.F. FOR. Craniofacial foramen

CHO. Choanae

CH. TYM. Chorda tympani

COC. GR. Cochlear groove

COL. AUR. Columella auris

COL. ROD. Columella rod

CON. BAN. Connective tissue band

C.N. Concha nasalis

COP. Copula

COP. I. First copula

COP. II. Second copula

CRAN. RIBS. Cranial ribs

CU. ANT. Cupola anterior of the nasal capsule

D.C.-C.C. Dorsal cochleo-canalicular commissure

DUCT. END. Ductus endolymphaticus

D.L.N.G. Duct of the lateral nasal gland

D.N.L. Ductus naso-lacrimalis

E.M. Eye-muscle

EPI. BRAN. Epibranchial

EPI. HY. Epihyal

EXT. COL. Extracolumella

F. Fontanelle.

FAC. NER. Facial nerve

F. PL. Footplate of the columella auris

FOR. ABD. Foramen for the abducent nerve

FOR. ACU. Foramen acusticum

FOR. B. CN. Foramen behind the concha nasalis

FOR. CAR. Foramen caroticum

FOR. C.T. Foramen in lower jaw for chorda tympani

FOR. END. Foramen for ductus endolymphaticus

FOR. FAC. Foramen for the facial nerve

FOR. HYPOP. Foramen hypophyseos

FOR. MAG. Foramen magnum

FOR. NC. Foramen for the tip of the notochord

FOR. OCC. Foramen for the oculomotor nerve

FOR. OLF. EV. Foramen olfactorium evehens

FOR. OPTH. Foramen for the ophthalmic artery

FOR. OVAL. Foramen ovale

FOR. PRO. Foramen prooticum

FOR. PERI. Foramen perilymphaticum

FOR. PROF. Foramen for the profundus nerve

FOR. R.M.N. Foramen for the ramus medialis nasi

FOR. TRO. Foramen for the trochlear nerve

FOR. VAG. Foramen for the vagus nerve

F.P.E.C.C.T. Foramen in the processus extracolumellaris for the chorda tympani

F.S.N.A. Fenestra septi nasi anterior

F.S.N.P. Fenestra septi nasi posterior

G. GAS. Ganglion Gasseri

G. GEN. Ganglion geniculatum

G. JUG. Ganglion jugulare

G.L.N.C. Groove lodging the notochord

GLOSS. Glossopharyngeal nerve

G. PET. Ganglion petrosum

G.Q.J. Groove in the pars quadrata for the quadratojugale

HYOM. Hyomandibular nerve

HYP. Hypoglossal nerve

HYP. FOR. Hypoglossal foramen

VOL. 34 1953

HYP. HY. Hypohyal
HYP. PIT. Hypophysial pit.
HYP. ROOF. Hypophysial roof
HYP. ROOTS. Hypoglossal roots
HUX. FOR. Huxley's foramen
INC. MET. Incisura metotica
INC. PRO. Incisura prootica
INF. POL. COM. Infrapolar commissure
INF. POL. PROC. Infrapolar process
INT. CAR. Internal carotid artery
I.S. Interorbital septum
LAT. CAR. FOR. Lateral carotid foramen
LAT. CAR. INC. Lateral carotid incisure
LAT. ABD. COM. Lateral abducent commissure
L.R. ACR. CAR. Lower region of the acrochordal plate
LS. Lens
MAX. TUR. Maxilloturbinal
M.C. Meckel's cartilage
MEM. Membrane
MET. CAR. Metotic cartilage
NA. SA. Nasal sac.
NC. Notochord
N.C.S.W. Nasal capsule side wall
N.L.D. END. Notch lodging the ductus endolymphaticus
N.L.O.N. Notch lodging the optic nerve
N.L. OP. N. Notch lodging the ophthalmic nerve
N.L. 7. N. Notch lodging the facial nerve
N.L. 9. NER. Notch lodging the glossopharyngeal nerve
N.L. 10. NER. Notch lodging the vagus nerve
NOT. RAT. POU. Notch for Rathke's pouch
N.S. Nasal septum
OC. ARC. Occipital arch.
O.C. Occipital condyle
OCC. Oculomotor nerve
OLF. Olfactory nerve
OP. AR. Ophthalmic artery
ORB. NAS. FIS. Orbitonasale fissure
ORB. PROC. Orbitocapsular process
OR. SI. Orbital sinus
OS. UNC. Os uncinatum
PAR. CAR. Parietotectal cartilage
PARS. CAN. Pars canalicularis
PARS. COCH. Pars cochlearis
PARS. QUAD Pars quadrata
P.D.P. TRAB. Postero-dorsally directed process of the trabeculae
PHAR. BRAN. Pharyngobranchial
PHAR. HY. Pharyngohyal
PIL. ANT. Pila antotica
PIL. ANT. SPU. Pila antotica spuria
P.L.P.C. Processus lateralis partis cochlearis
OL. SUP. SEP. Planum supraseptale
POL. CAR. Polar cartilage
POST. ORB. CAR. Postorbital cartilage
POST. PROF. COM. Postprofundal commissure
PRECAR. COM. Precarotid commissure
PRE. END. COM. Pre-endolymphatic commissure
PRE. NAS. Prenasal process
PRE. OPT. RT. Preoptic root of the orbital cartilage
PRO. EXT. COL. Processus extracolumellaris
PROC. INF. COL. Processus infracolumellaris
PROC. LING. Processus lingualis
PROC. ORB. QUAD. Processus orbitoquadratus
PROC. OTIC. Processus oticus
PROC. RET. Processus retroarticularis
PROC. SUP. COL. Processus supracolumellaris
P. SUP. COL. LAT. Processus supracolumellaris lateralis
PROC. SUP. COL. MED. Processus supracolumellaris medialis
RE. FOR. HYPOP. Remnant of the foramen hypophyseos
RE. ACR. CAR. Remnant of the acrochordal cartilage
RET. Retina
R.L.N. Ramus lateralis nasi
R. MAN. Ramus mandibularis
R. MAX. Ramus maxillaris
R.M.N. Ramus medialis nasi
R. PAL. Ramus palatinus
R. PROF. Ramus profundus
RUD. FLOOR. Rudimentary floor to the nasal capsule
S.C. ARC. Supracolumellar arcade.
SC. CA. Sclerotic cartilage
S.T.P.A. Section through the pila antotica

STAP. OSS. Stapedial ossification
S.T.S.C.P. Section through subcapsular process
S.F. Sphenoid fontanelle
S.P.H. COM. Sphenethmoid commissure
1. SPIN. NER. First spinal nerve
STY. Stylohyal cartilage
SUP. ORB. CAR. Supraorbital cartilage
SUP. POL. CA. Suprapolar cartilage
TEC. SYN. Tectum synoticum
TRAB. Trabeculae
TRAB. COM. Trabecula communis
TRO. Trochlearis nerve
VAG & ACC. Vagus plus accessory nerve

VOL.
34
1953

ON THE "HORIZONTAL PIT-LINE" IN TELEOSTOMIAN FISHES

BY

NILS HOLMGREN

"In gnathostomian fishes two types of cheek-line systems are present. 1) One type with undifferentiated jugal line (*Holocephalia, Rajiformes, Arthrodira*) and 2) another with a differentiated jugal system (all other Gnathostomians)" (HOLMGREN and PEHRSON, 1949, p. 311).

The characteristic of the first of these two groups is that the cheek is devoid of sensory lines behind the oral line or between this line and the mandibular line. There is seen nothing of vertical and horizontal pit-lines, nor is there any preopercular line developed. Any such lines in these fishes, indicated in the literature are pure constructions. (Compare HOLMGREN and PEHRSON, 1949).

In the second of the two groups the jugal line is composed of three sections, called (by HOLMGREN and PEHRSON) respectively the jugal 1 (j_1), the jugal 2 (j_2) and the jugal 3 (j_3) (fig. 1). STENSIÖ calls them the anterior, middle and posterior divisions of the supramaxillary line (hc_1, hc_2, hc_3 respectively). In the embryos of sharks (*Squalus*), where the jugal line is most typically developed, the first division, which is horizontal, *caudally bends down to the lower jaw*, there forming the primary oral line (called by STENSIÖ the postmaxillary line: *orp.*) (H. and P. figs. 2 and 3, p. 252 and 253). The second section of the jugal line (j_2) is in embryos and also in adult *not* continuous with the first division or with the primary oral line [1]. It runs dorsad *in front of the spiracle*, where the line abruptly bends ventrad. The dorsally directed portion of this bent line is the jugal 2 (j_2, hc_2), the posterior shank being the jugal 3 (called by STENSIÖ the preopercular line). The jugal 2 generally develops into a pit-line (called by me, who described it, the "middle cheek-line"). The jugal 3, generally forming a sensory canal, ends level with the first division, where a posterior knob or twig marks the limit between the third division and the preoperculo-mandibular line.

An *important statement* is that the *jugal 1 division carries the (primary) oral line* and that the second division (j_2) thus has nothing to do with the primary oral line. (Compare H. and P. figs. 1, 2, 3).

The cheek-line system in the recent *Dipnoi* is of the greatest interest and probably furnishes the key for the understanding of the cheek-line system in the teleostomian fishes. On the cheek of *Neoceratodus* as well as of *Protopterus*

[1] My reconstructions (HOLMGREN, 1940) of the cheek lines in *Squalus* embryos are not quite correct, as stated in H. and P., p. 250.

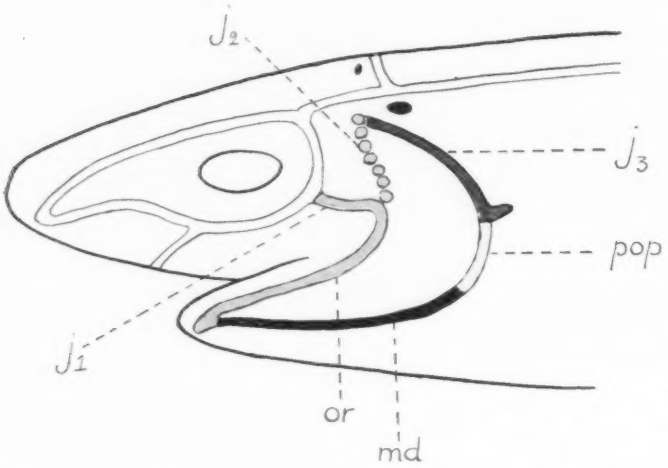

Fig. 1. Diagrammatical picture of the conditions of the cheek-line system in sharks. j_1 (orange), j_2 (gray) and j_3 (blue): the three divisions of the jugal line. *pop* (yellow): the preopercular line (prospective in sharks). *md* (black): the mandibular line; *or*: the primary oral line.

VOL. 34 1953

there are two sensory canals and three pit-lines present, the pit-lines lying in the space between the canals (HOLMGREN, 1942). The canals are the jugo-oral canal and the jugo-preoperculo-mandibular one. The pit-lines are the "primary mandibular" line, the "vertical pit-line" and the "secondary oral line" or quadrato-jugal line (fig. 2). The painstaking ontogenetical investigation on the sensory line system in *Neoceratodus* as well as in *Protopterus*, carried out by PEHRSON (1949), has shown that GREIL's picture of the sensory lines of the cheek of an *Neoceratodus* embryo is in every respect erroneous, and that all conclusions drawn from that picture must be incorrect. PEHRSON (1949) has followed the development of the cheek-lines by steps. The jugal system of young embryos (11.5 mm) belongs clearly to the differentiated type and consists of three divisions (j_1, j_2, j_3), of which the foremost (j_1) already in the 12 mm stage connects with the infraorbital line and with the primary oral line. The second division (j_2) of the jugal system is raised up dorsad to level with the lower outline of the eye. Then the line abruptly bends down forming the third division (j_3), which ends with a knob (opercular line), similar to that in *Squalus*. This knob marks the boundary between the jugal 3 division and the preoperculo-mandibular line. The second jugal division (j_2) ultimately develops into a pit-line viz. "the vertical pit-line." Ventrally this division looses its connection with the first division (j_1). At the dorsal ends of the jugals 2 and 3 a secondary connection is formed between these ends and the postorbital line. This connection is effected by means of a separately developed short line section (with but one neuromast). This section HOLMGREN and PEHRSON called the

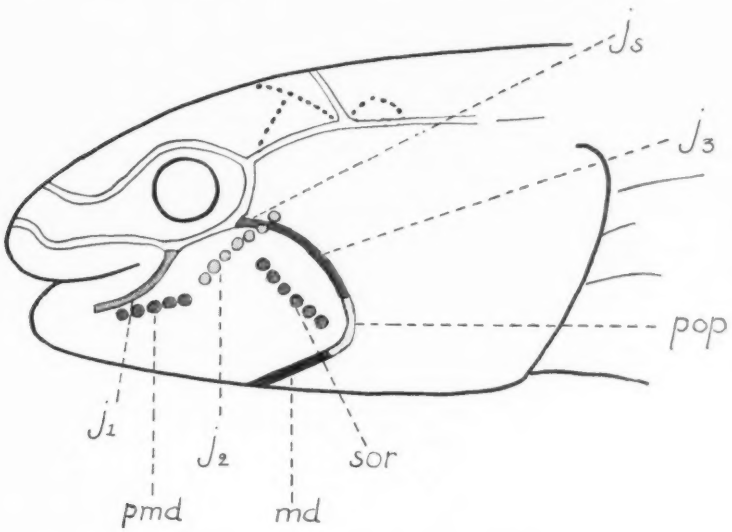

Fig. 2. Diagrammatical picture of the conditions of the cheek-line system in *Neoceratodes*. Lettering and colours as in fig 1, but thereto, *pmd* (green): the "primary mandibular line"; *sor* (brown): secondary oral line. j_s (red): secondary jugal line.

secondary jugal line (j_s). This line division forms the immediate continuation frontad of the j_3.

Immediately behind the oral line, where it bends around the mouth angle, lies a short pit-line called by me the "primary mandibular line" (HOLMGREN, 1942). PEHRSON (1949) has followed its development in *Neoceratodus* as well as in *Protopterus*. It forms independently behind the primary oral line or canal. In young stages of *Neoceratodus* it is parallel to the oral line; later it becomes directed more horizontally. It is quite independent of the vertical pit-line, (called by PEHRSON the "dorsal part of the primary mandibular line") with the lower end of which it, however, may connect in a semiadult stage (2 ¼ year old).

A short distance in front of the preoperculo-mandibular canal a pit-line is developing already in the 12 mm stage (of *Neoceratodus*). This rudiment is, as far as PEHRSON's dravings show, independent of the vertical pit-line rudiment. It retains this independence throughout the entire development. This pit-line was called by me the secondary oral line (HOLMGREN, 1942). It corresponds to the quadrato-jugal line of the authors. It may, however, be noted that in a certain stage of development (16.5 mm *Neoceratodus*) the upper end of the quadrato-jugal and the lower end of the vertical pit-line are closely together, so that it looks as if the former should be derived from the latter. (Compare with *Dipterus* fig. 3).

The sensory line system on the cheek of recent lungfishes thus consists of

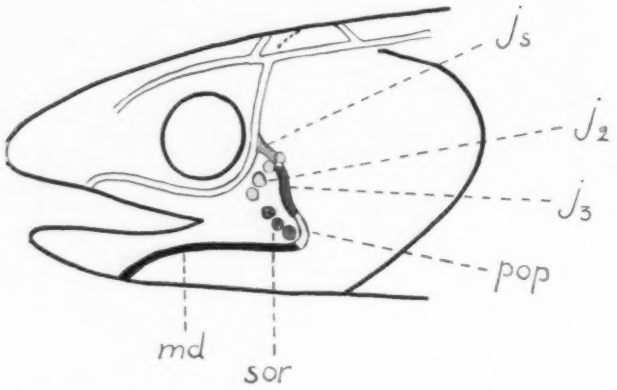

Fig. 3. Diagrammatical picture of the conditions of the cheek-line system in *Dipterus*. Lettering and colours as in fig. 2.

1) the first division (j_1) of the jugal line or canal with the primary oral line or canal. 2) The second division of the jugal line (j_2) or vertical pit-line. 3) The third division of the jugal line (j_3). 4) The secondary jugal line (j_s) connecting the upper end of the j_3 with the postorbital canal. 5) The preoperculo-mandibular line. 6) The primary mandibular line just behind the primary oral line and 7) the secondary oral line or quadrato-jugal line in front of the (secondary) mandibular line[1].

The conditions in the recent lungfishes provide the key for the understanding of those in telostomian fishes (and also in urodeles) and must not be overlooked.

The understanding of the transition from recent lungfish conditions to those in Crossopterygians is faciliated by the line pattern in the extinct lungfish *Dipterus* (fig. 3). In this fish the primary oral and the primary mandibular lines are absent. Perhaps the explanation is that these lines have been running in soft skin without closely underlying bone. Those parts which are preserved show, however, perfectly Crossopterygian conditions, viz. a jugal system in which the primary oral and primary mandibular lines are missing (fig. 4). The jugal system, thus, consists of the jugal 2 and the secondary jugal line (j_s). The jugal 3 begins frontally about where it is crossed by the jugal 2 and extends caudad into the preoperculum. There is, however, no pronounced limit between the jugal 3 and the preoperculo-mandibular line. As we already have seen there is such a pronounced limit in sharks and recent Dipnoans, and we must assume that the preopercular line in Crossopterygians also dorsally met

[1] The jugal 1 + primary oral line is called by STENSIÖ the postmaxillary line, dorsal part; the primary mandibular line is called the postmaxillary line, ventral part. With the latter the jugal 2 line has been mixed up, the quadrato-jugal line being called the middle supramaxillary line (hc_2). These mistakes have arisen from the use of GREIL's figure as basis for hypothetic ontogenetical stages.

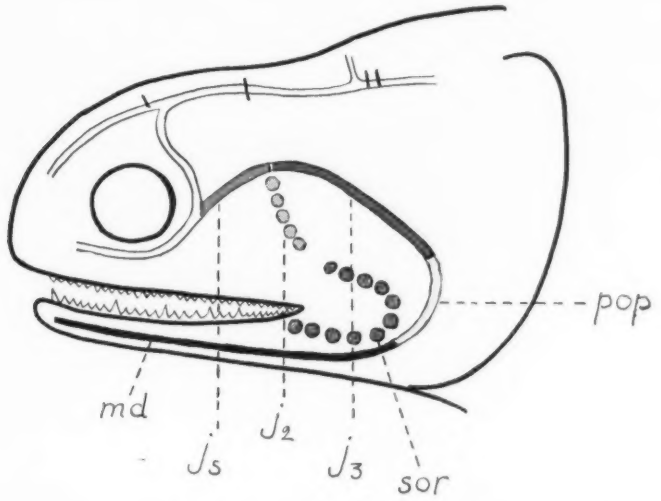

Fig. 4. Diagrammatical picture of the conditions of the cheek-line system in *Holoptychius*. Lettering and colours as in figs. 2 and 3.

the third jugal division (j_3), even if there is no visible limit. In recent Dipnoans the limit is only determinable in the embryos. Perhaps the same was the case in the Crossopterygians.

From what previously has been said about the canal which originally was called the "jugal canal" in Dipnoans and Crossopterygians, it must follow that this canal can not be considered to be a preopercular canal connected with the postorbital canal in front of the spiracle instead of with the temporal canal behind the spiracle as in higher fishes. The ontogenetical researches on Dipnoans show that the "jugal canal" consists of a jugal 3 line with three neuromasts connected caudally with the preoperculo-mandibular line and frontally with the secondary jugal line (with one neuromast). Considering the ontogenetical development the "preopercular canal" of the terminology used by STENSIÖ and LEHMAN should be composel of 1) the more or less vertical part of the preopercular canal, 2) the jugal 3 canal and 3) in front of that canal division again a preopercular canal portion. But such a preopercular canal is very improbable and its existence can not be maintained without improbable assumptions, such as that the jugal 3 has got absorbed as a component of the "preopercular canal" and that the jugal 2 has dwindled to nothingness. Such assumptions lack any support in the ontogeny.

And now we are prepared for the question of the "horizontal pit-line. STENSIÖ (1947) has homologized it with the first division (hc_1) of the "supramaxillary line," that is with the jugal 1 of my description. It is obvious that this homology cannot be supported any more as the ontogenetical researches on *Amia* (H.

and P., 1949, p. 285) show that the posterior part of the "horizontal pit-line" *is* the jugal 3 (hc_3) and the upper part of the "vertical pit-line" the jugal 2 (hc_2)[1]. The continuation ventrad of the latter is the secondary oral line or quadratojugal line and not the primary oral line (*orp.*), as has been suggested. In an 8 mm embryo of *Amia* the anterior part of the "horizontal pit-line" has not yet appeared. The anterior part of the "horizontal pit-line" thus remains as the hc_1 of STENSIÖ. But is that really the hc_1, i.e. the jugal 1 of my description? The typical jugal 1 is in recent fishes only present in sharks and lungfishes and it is consequently from these fishgroups we have to gather the full morphological and ontogenetical characteristics of these lines. In the adult fishes the jugal 1 is a canal connecting the infraorbital canal with the primary oral canal. In embryos the j_1 lies level with the lower end of the j_2 line. None of these characteristics applies to the "horizontal pit-line", which is joined with the upper end of the j_2 and has no relation to any primary oral canal. Therefore I must reject the interpretation of the "horizontal pit-line" as the jugal 1 division of the original differentiated jugal line. What is then the anterior part of the "horizontal pit-line"? H. and P. (1949) have concluded (p. 283) that this line is the secondary jugal line, which in lungfishes and Crossopterygians is developed as a canal, but in Palaeoniscids, Holosteans and Teleosts is developed as a pit-line (fig. 5). This conclusion has not been accepted by STENSIÖ's scholar LEHMAN[2], because the latter has found (1952)—in the coelacanthid *Whiteia woodwardi* a short horizontally located pit-line below the jugal canal and in front of the vertical pit-line. In a specimen of *Whiteia tuberculata* the two pit-lines are differently arranged. The "horizontal" line has not an horizontal position and is situated at the lower end of the vertical pit-line on the quadrato-jugal bone. This latter line, however, may be another pit-line than the "horizontal" in the *Woodwardi*. Why is the horizontal line in *Whiteia* then considered to be homologous with the "horizontal pit-line" (hc_1, j_1)? Only because the line is horizontal and located in an approximate way where a *hypothetical* "horizontal pit-line" has been drawn on the cheek of *Nesides*. The reasons why I do not consider this line to be the j_1 line are: 1) Among choanate fishes the genuine j_1 (hc_1) division of the jugal series is only found in the recent lungfishes. 2) In the Crossopterygians the original j_1 (hc_1) is always absent. 3) In the lungfishes there is behind the primary oral line (j_1) another line, the primary mandibular line (*pmd*), which must not be omitted in the discussion. This line in young stages of development runs parallel with the primary oral line (*orp.*). Later it becomes more and more

[1] This pit-line does not develop together with the preopercular line as supposed by STENSIÖ. PEHRSON (1940) did not follow the development of the horizontal and vertical pit-lines in *Amia*. These primordia are not indicated in the figures, used by STENSIÖ to demonstrate his opinion.

[2] Etude complémentaire des poissons de l'eotrias de Madagascur. Kungl. Svenska Vetenskapsakademiens handlingar 4, Sér. Band 2. N° 6, 1952.

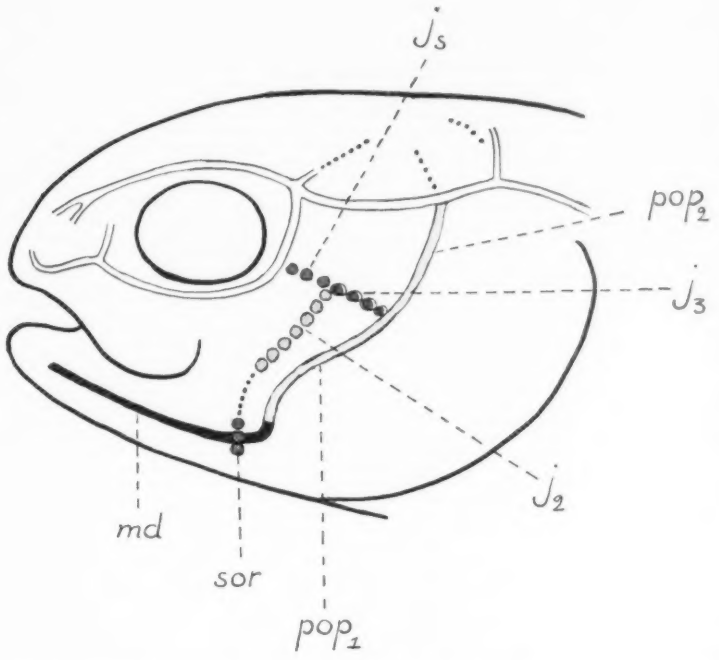

Fig. 5. Diagrammatical picture of the conditions of the cheek-line system in *Amia*. pop_1 = primary part of the preopercular line. pop_2 = secondary part of the same. Other letterings and colours as in figs. 2, 3, 4.

horizontal with its posterior upper part nearly joining the lower end of the j_2 section (vertical pit-line). This primary mandibular pit-line, somewhat dislocated dorsad, explains the pit-line on the cheek of *Whiteia* better than any "horizontal pit-line" as jet can do. 4) LEHMAN says that the pit-line in question "ne peut être assimilée en raison de la direction à la ligne moyenne de la joue de HOLMGREN et PEHRSON (1949, fig. 38: j_2)." I must confess that I had never imagined the possibility of such an explanation.

In the preceding pages I have summarized the essentials of the comparative anatomy of the sensory lines of the cheek in fishes, I will here only emphasize two results: 1) The "preopercular" canal in front of the spiracle is no preopercular canal but consists of the jugal 3 line together with the secondary jugal line (j_3). 2) The anterior portion of the "horizontal pit-line" is the secondary jugal line, the posterior portion is the jugal 3 line. The "horizontal pit-line" in *Whiteia* represents probably the primary mandibular line in *Neoceratodus* (and *Protopterus*).

A full preopercular line, consisting of a ventral, primary (*pop*, pop_1 and a

dorsal secondary part (*pop*$_2$) is present only in *Palaeoniscids, Holostei* and *Teleostei*. The lower teleostomian fishes have only the primary part.

My results in this paper, like those of HOLMGREN and PEHRSON (1949) are founded upon structures really present in adult specimens or in their embryos. The fact that it never has been necessary to resort to constructions or assumptions of hypothetic sensory lines seems to strengthen the interpretation.

VOL
34
195

ON THE DEVELOPMENT OF DIENCEPHALIC NUCLEI AND CERTAIN MESENCEPHALIC RELATIONS IN *LEPIDOCHELYS OLIVACEA* AND OTHER REPTILES[1]

BY

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VOL. 34 1953

CONTENTS.

I. Literature and Introduction 155
II. Material and Methods 157
III. Results 158
Hypothalamus 167
Epithalamus and Thalamus 171
Synencephalon 174
IV. Discussion 177
Hypothalamus 179
Epithalamus and Thalamus 179
Synencephalon 180
V. Summary 180
VI. Abbreviations 181
VII. List of Material 183
VIII. Bibliography 188

I. LITERATURE AND INTRODUCTION

Very little is yet known about the morphogenesis of the diencephalic nuclear systems in reptiles. Thus one of the few contributions to the literature was made by RENDAHL (1924) who, merely to supplement his main studies on the development of diencephalic nuclei in *Gallus gallus*, made some brief comparisons with similar phenomena in reptiles. KUHLENBECK (1931) has studied similar problems in embryonic and adult material of different reptiles. And WINGSTRAND (1951) traced the ontogeny of Rendahl's 'Kernanlage a' and also of a few other hypothalamic nuclei in connection with his investigation of the hypophyseal development in birds.

[1] The cost of this investigation was defrayed by grants from the *Swedish Natural Science Research Council, Lars Hierta's, Helge Ax:son Johnson's* and *Magnus Bergvall's Foundations* in Stockholm.—The investigation began in 1932 and was resumed in 1948.

In adult or at any rate young reptiles, on the other hand, a large number of researchers have tried to elucidate the nuclear relations in the diencephalon and mesencephalon; and this was often combined with a description of the anatomy of the nerve fibres in these regions. EDINGER (1899) made a contribution of fundamental importance by his study of the nuclei and their connecting fibres in *Varanus* and other species[2]. In 1913 DE LANGE published a monograph on nuclei and fibres in i.a. *Varanus salvator*, listing the terms used by various authors to designate different thalamic nuclei and describing their relations to one another in reptiles and mammals.

The following of the more recent publications may be mentioned: CROSBY's (1917) on nuclear relationships in *Alligator mississippiensis;* BECCARI's (1923), in *Lacerta muralis;* CAIRNEY's (1926), in *Sphenodon punctatum;* HUBER & CROSBY's (1926, 1929, 1943), in *Alligator* and other species; SHANKLIN's (1930, 1933), in *Chamaeleon vulgaris;* PAPEZ's (1935), in *Chelone midas,* other turtles and reptiles, GREVING (1935), ROSE (1935) and SPATZ (1935) in some higher vertebrates, ARIËNS KAPPERS, HUBER & CROSBY's (1936)[3], in various reptiles; CURWEN & MILLER's (1939) in *Pseudemys scripta;* DIEPEN's (1943), in *Lacerta agilis;* WARNER's (1942, 1947) in *Natrix sipedon* and in *Crotalus adamanteus* etc.

Along with the literature on reptilian development, attention has also been paid to investigations of the ontogeny of the corresponding parts of the brain, which have been made in mammals and man by the following authors: DROOGLEVER & FORTUYN (1912), rabbit; GILBERT (1935), man; ROSE (1942), rabbit; COOPER (1950), man; BENGMARK, HUGOSSON & KÄLLÉN (1953), mouse. In addition reference is made to BERGQUIST (1932, 1952 a—c and 1953).[4]

In the earliest development of the embryonic vertebrate brain one can distinguish, as shown in BERGQUIST & KÄLLÉN's (1935 c) summarizing paper, three characteristic phases. They can be associated with the appearance of transverse formations arranged segmentally in the neural folds and neural tube; and, in the order of their appearance, these structures are called proneuromeres, neuromeres and transversal bands. Just after the transversal bands have developed there emerges in the cellular matrix of the ventricular wall a longitudinal banding which, criss-crossing the transverse bands, gives rise to a chequered pattern of migration areas, i.e. budding centres for the cerebral nuclei. During later stages of development the transverse banding may be suppressed by the longitudinal bands. These bands approximately correspond to HIS-HERRICK's

[2] I want to refer to a summary of the older litterature by HUBER & CROSBY (1926).

[3] Their bibliography i.a. is well worth perusal.

[4] From time to time reference is made to papers that have not been published at the time of writing and may be published after this paper. This is because the papers in question were submitted for publication in 1951 and later and will only be printed in the near future.

columns, which, according to our opinion, have lost their physiological properties rostrally.

The definitive arrangement in the ventricular wall and differentiation of the nerve cells may be regarded as the last phase in the final establishment of the brain. This process gives origin to the more or less compact and well demarcated clusters of nerve cells, the so-called cerebral nuclei, and to the complex filtering and fascicular system of nerve fibres, and to other structural units. The cerebral nuclei are on the whole either identical to the migration areas, as in *Petromyzon* and amphibians, or they arise through subdivision of one or more migration layers (migr I, II, etc.), i.e. layers of cells, which have migrated successively from the ventricular surface. The migration areas and migration layers (migr I, etc.) are of significance for the homologization of cerebral nuclei (cf. BERGQUIST & KÄLLÉN, 1953 c).

Analysing the variability of hypothalamic nuclei in adult animals, FEREMUTSCH (1949) found that while the cells often changed in size they showed negligible individual variations in structure and shape. Between the cerebral nuclei of the left and those of the right side he observed no significant differences.

In more recent publications FEREMUTSCH (1949, 1951) emphasized the necessity of expressing the cellular arrangement in the ventricular wall in terms of larger cytoarchitectural units. Otherwise, stated Feremutsch, the considerable individual variation could easily become misleading. Thus, for example, he alleged that BROCKHAUS (1942) had been wrong in going into details about a multitude of subdivisions of the nuclear regions ordinarily recognized (cf. also FEREMUTSCH & GRÜNTHAL, 1952).

The present investigation seeks in the first place to illuminate the problem of the development of diencephalic brain nuclei. Some similar problems in the mesencephalon are considered too. While most of the work was done on embryonic material from *Lepidochelys olivacea,* other reptilian material was used partly for control purposes and partly to provide a wider orientation. A monograph or a variation analysis of different types of reptilian brains are not to be given. Moreover, since comparative studies were made on avian, mammalian and human materials, it is to be hoped that this investigation will contribute something of value to the homologization of brain nuclei in other vertebrates. This problem I shall discuss in a forthcoming paper.

II. MATERIAL AND METHODS

The material consisted of a closely spaced embryonic series of *Lepidochelys olivacea.* Full data on this and other reptilian materials used are given in table 1.

Graphical and wax-plate reconstructions were made by the technique adopted in preceding investigations (BERGQUIST, 1952 b, etc.). For terminology and abbreviations consult BERGQUIST (1952 b and c) and BERGQUIST & KÄLLÉN (1953 c).

In this paper the fibre connections of the cerebral nuclei have only been investigated in a few special relations. Instead I should like to refer to the fibre-anatomical papers mentioned in the introduction. Particularly, I want to refer to the monograph by ARIËNS KAPPERS, HUBER & CROSBY (1936). In my forthcoming paper, mentioned above, I shall look more closely into the fibre-anatomical conditions and other histo-anatomical facts of importance for the identification and homologization of the diencephalic nuclei in different animals and man.

The HERRICK-school maintains that morphological research should be extended to embrace the functional face of development. These scientists have studied the problems i.a. in amphibians of later stages and adults. The questions are of great importance and have been very much discussed in recent years, but neither KUHLENBECK (1926) nor LE GROS CLARK (1936), among others, have been able to confirm this opinion. In some previous papers KÄLLÉN and I described the early development of the cerebral tube in a great deal of vertebrates. However, our investigations have not fully unravelled the problem which, in our view, remains unsolved. I should like to refer the reader to BERGQUIST (1952 c, p. 12) for further statement on the subject.

III. RESULTS

Lepidochelys olivacea—10-day, 11-day and 12-day stage (fig. 1 a—d)

The external topography of *a.c.hyp.* is demarcated by fovea hypothalamica at the top and by another smaller groove at the bottom. RENDAHL called this furrow 'die intermammilläre Furche' and has designated it with the letter x.

At the 10-day stage *a.d.tel.* had already become clearly demarcated from *a.r.th.* As from the 12-day stage there is a boundary region between *a.d.tel.* and *a.r.th.* As KÄLLÉN stated (1951 a) such an area arises during the later stages of ontogeny in lower animal species. Here it will be called area intercalata (*a.intercal.*) The homologization of this area in different lower vertebrates has been discussed by KÄLLÉN (1951 c).

As at the 10-day stage (BERGQUIST, 1952 c, fig. 5), *a.com.post.* displays a tendency to divide into a dorsal and a ventral region. A distinct partition is visible at the 12-day stage. Not until the 9-day stage has transversal band 7 divided into a medial strip consisting of area dorsalis mesencephali, pars caudalis (*a.d.mes., p.caud.*), and a lower strip, area ventralis mesencephali, pars caudalis (*a.v.mes., p.caud.*). It is interesting to note that at the 12-day stage transversal band 7 still enters the mesencephalic roof, as becomes evident by observing the external margins of the band as well as by its topography in the ventricular gray (see fig. 1 a and b). Concurrently the deep isthmic constriction has compressed the band.

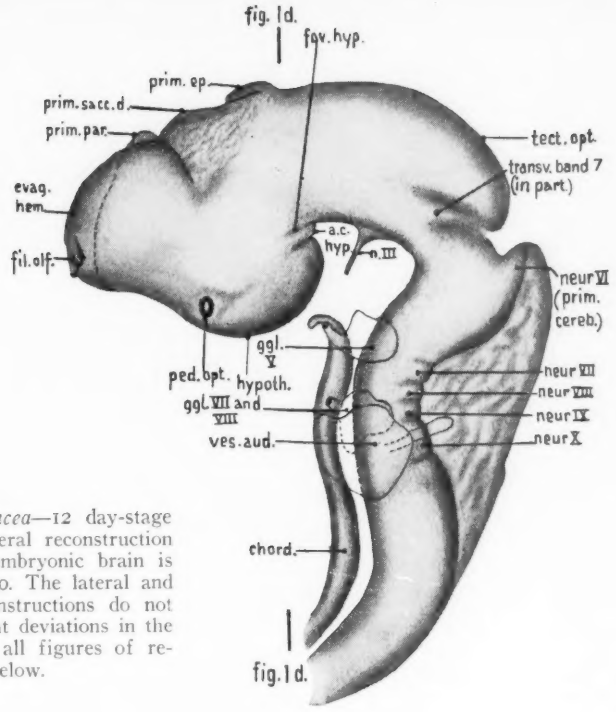


Fig. 1 a. *Lepidochelys olivacea*—12 day-stage (10,5 mm). The externo-lateral reconstruction of the right half of the embryonic brain is reversed. Magnification × 20. The lateral and medial aspects of the reconstructions do not exactly conform due to slight deviations in the projection used. Applies to all figures of reconstructions below.

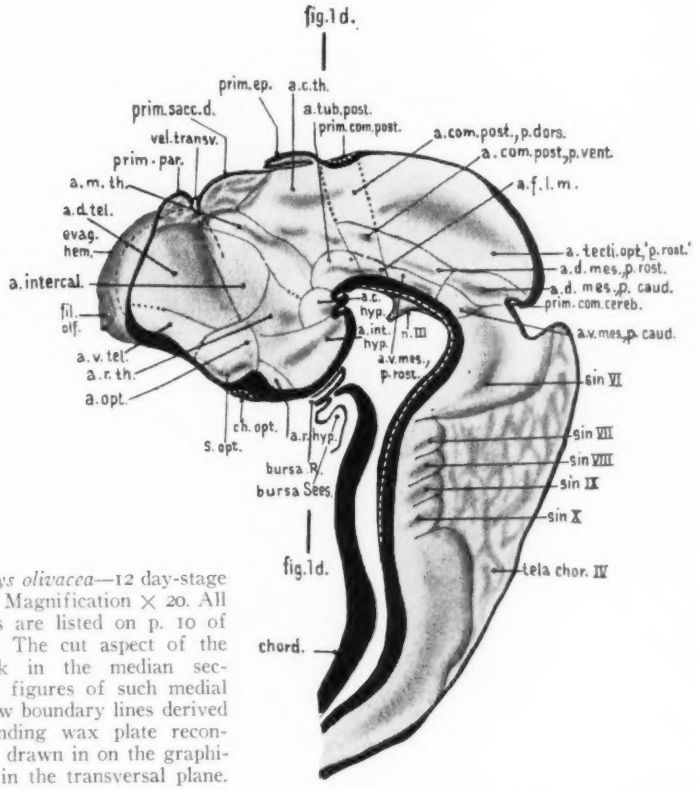


Fig. 1 b. *Lepidochelys olivacea*—12 day-stage (10,5 mm). Graph.i. Magnification × 20. All the migration areas are listed on p. 10 of BERGQUIST, 1952 c. The cut aspect of the wall appears black in the median section. Applies to all figures of such medial aspects below. A few boundary lines derived from the corresponding wax plate reconstruction have been drawn in on the graphical reconstructions in the transversal plane.

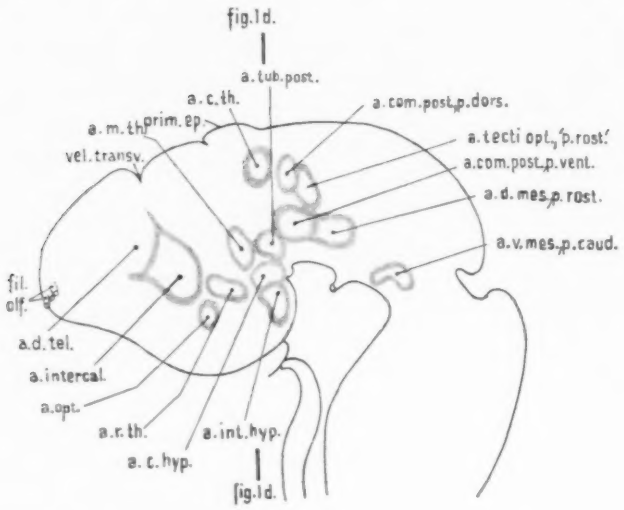


Fig. 1 c. *Lepidochelys olivacea*—12 day-stage (10.5 mm). Graph.nuclei. Magnification × 20. The migration cell clusters are seen in lateral projection. The reconstruction is reversed.

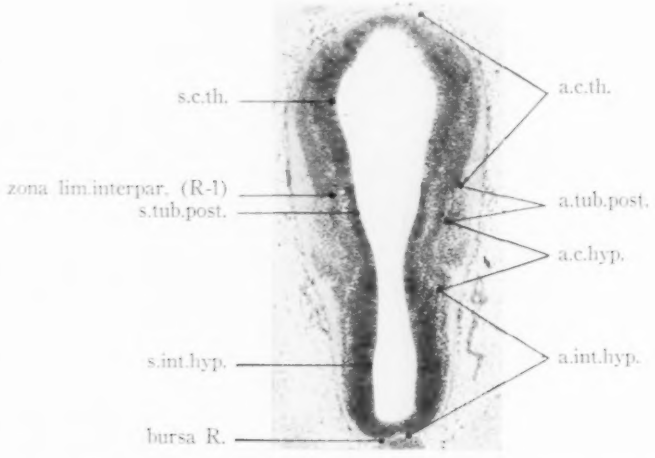


Fig. 1 d. *Lepidochelys olivacea*—12 day-stage (10.5 mm). Cross section, marked in fig. 1 a—c. Magnification × 40.

As BERGQUIST (1952 c) has demonstrated, one can observe already at the 8-day stage a first diffuse migration of cells from *a.tub.post.* as a *migr I.* At stages 10 and 11 days the aforementioned cell migration becomes more dense and appears contiguous with adjacent migrations from *a.c.hyp.* and *a.f.l.m.* At 12-day stage cells have also started to migrate rostrally in the hypothalamus, as well as in the thalamus, the synencephalic and the mesencephalic regions (see fig. 1 c and d).

VOL. 34 1953

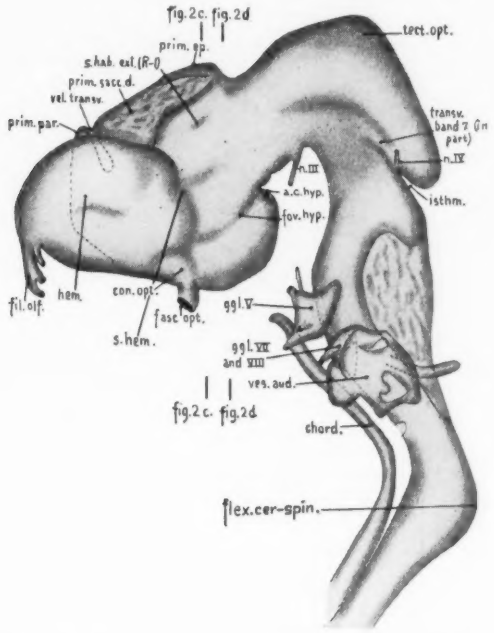


Fig. 2 a. *Lepidochelys olivacea*—14 day-stage. Graph.e.l.* Magnification × 16. In the rhombencephalon are remnants of the rhombomeres not marked.

Lepidochelys olivacea—13-day and 14-day stages (fig 2 a—d)

At the 13-day stage no new developments of significance have taken place. The telencephalic region, the chorioidal part of the dorsal diencephalon, and tectum opticum have greatly expanded in various directions. At this stage such growth is characteristic of the rostral embryonic brain.

Taking a ventral course from velum transversum, the so-called sulcus hemisphaericus has developed at the 14-day stage. Fovea hypothalamica runs even if interrupted along the dorsal margin of the hypothalamus to the optic cone region. The primordium of ganglion habenulae is marked off by an externo-ventral furrow which RENDAHL (1924) called sulcus habenularis externus (fig. 2 a and c, *s.hab.ext. R—l*). The ventral border of tectum opticum is also marked off by an external fold. What remains of transversal band 7 is similarly manifested externally and caudally by a fold originating at the isthmic fold and proceeding for a short distance morphologically ventrad. In the upper part of this fold the primordium of the trochlear nerve is visible for the first time in this series as a thin cord emerging from the cerebral tube.

Next to the primordial saccus dorsalis (*prim.sacc.d*) the presumptive ganglion habenulae has now been established in the dorso-caudal part of *a.c.th., p.dors.*

Ventrally on the ventricular surface this ganglion habenulae is marked off by sulcus subhabenularis (fig. 2 b and c), while the deeply cut proliferation furrow *s.m.th.* still passes through the middle of *a.m.th.'s* ventricular surface.

The longitudinal band forming *a.d.mes., p.rost.* in the dorsal region of the tegmentum continues without visible transition rostrad into *a.comp.post., p.vent.* which at this stage

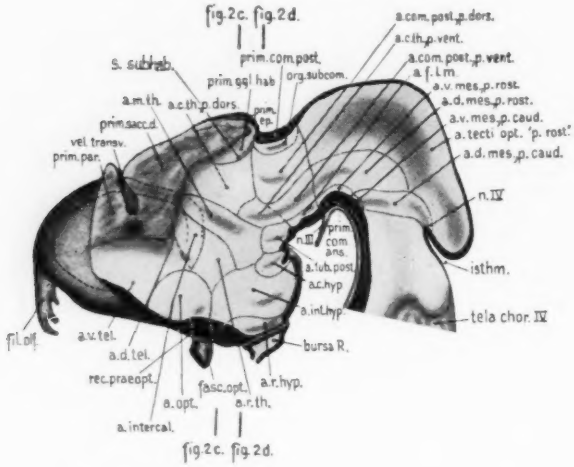


Fig. 2 b. *Lepidochelys olivacea*—14 day-stage. Graph.i. Magnification × 16. A few boundary lines in the transversal plane derived from the corresponding wax-plate rec. have been drawn in on the graphical reconstructions.

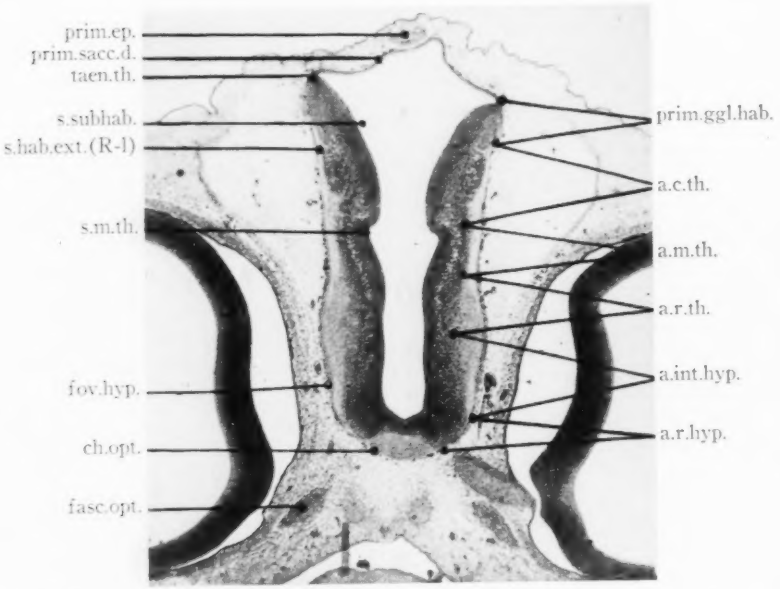


Fig. 2 c. *Lepidochelys olivacea*—14 day-stage. Cross section marked in fig. 2 a—b. Magnification × 30.

VOL. 34 1953

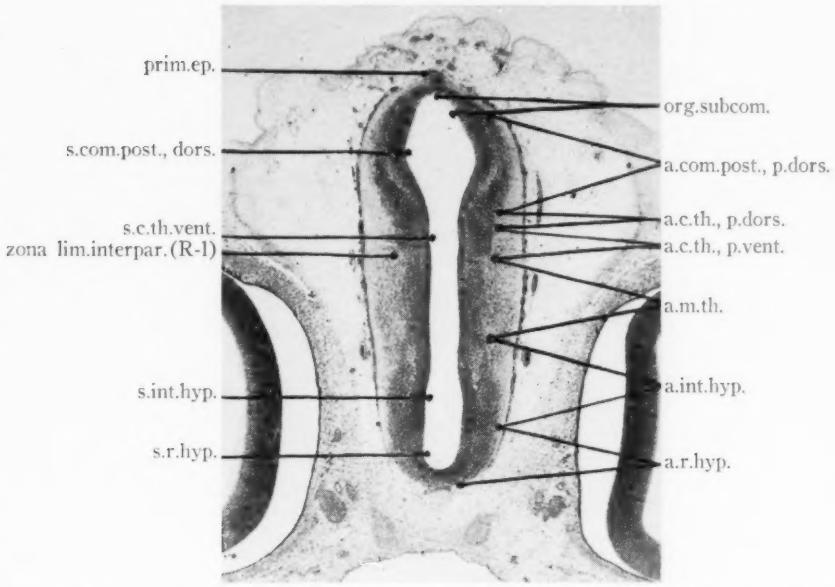


Fig. 2 d. *Lepidochelys olivacea*—14 day-stage. Cross section, marked in fig. 2 a—b. Magnification × 30.

is well established from the *a.com.post., p.dors.* above it. The organon subcommissurale has developed in the most dorsal region of the synencephalon. *A.c.th.* has separated into a ventral and a dorsal part, of which the former and also *a.com.post., p.vent.* and *a.f.l.m.*, are situated along the extension of the longitudinal band mentioned above. Morphologically ventral to it lie *a.tub.post.* and *a.c. hyp.* as well as the other hypothalamic zones, all of which are derivatives of the same longitudinal band as *a.d.mes., p.rost.* The band might in its entirety have arisen from the ventrolateral column (BERGQUIST & KÄLLÉN, 1953 b and c).

Cell migration has increased since the 12-day stage and can be seen in most migration areas, even if only small cell groups from stratum matricis are established in *a.r.hyp., a.int.hyp., a.c.th.* and *a.tecti opt.* At this time, too, a characteristic cytoarchitecture which will persist at subsequent stages is beginning to appear in a number of migration areas. Such is the case in the following regions for example: *a.c.th.* and *a.com.post.* The cells in *a.c.th.* begin to aggregate, forming masses with an oval cross-section (fig. 2 c; cf. fig. 5) and *a.com.post.* forms a laterally curved bulge (fig. 2 d).

The borderline between *a.m.th.* and *a.c.th.* is easily recognized by a very marked, elongated region in ventricular gray where tractus thalamo-mammillaris will lie (fig. 2 d). Comparatively poor in cells initially, this region was called zona limitans interparencephalica by RENDAHL (1924) and zona limitans intrathalamica by KUHLENBECK (1930). It marked off, according to KUHLENBECK, the dorsal thalamus from the ventral.

Lepidochelys olivacea—stages 15-28 days (figs. 3-7 a-h)

No significant developments have been added at the 15-day stage.

A.int.hyp. in the 16-day and 17-day stages tends to divide into a rostral and a caudal

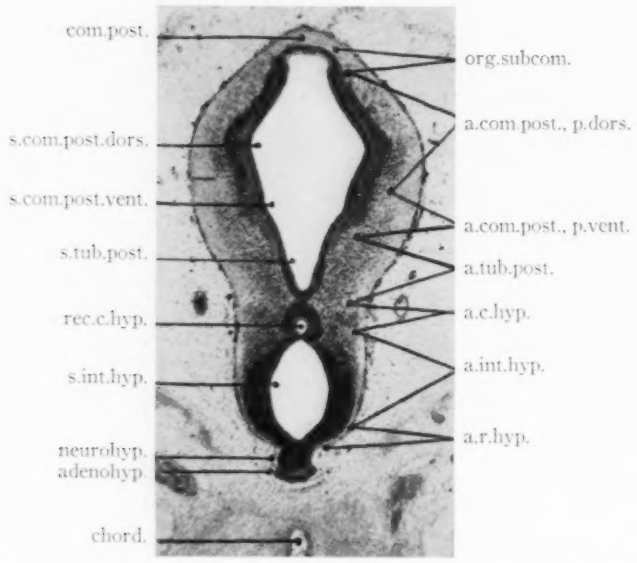


Fig. 3. *Lepidochelys olivacea*—17 day-stage (13 hl). Cross section in the caudal part of diencephalon. Magnification × 30.

portion morphologically. One can observe in *a.d.mes., p.rost.* PALMGREN'S (1921) 'lateral and medial cell columns'.

In the below chiefly the 28-day stage will be described in detail; and, unless the circumstances demand it, younger stages will not be discussed.

An inspection of the embryonic brain's lateral configuration at the 28-day stage (fig. 7 a) reveals that both the region of stria medullaris and the great bundles of ascending optic fibres (*ascend.opt.fibr.*) are bordered by clearly visible folds. And as from the 22-day stage the commissura habenularum (*com.hab.*) bulges out dorsolaterad. The entire ventral border of tectum opticum is marked off by a partially deep fold and by the caudal margin of the transversal band 7. The latter also constitutes a mesencephalic borderline against the rhombencephalon.

At the 20-day and later stages mitotic division can no longer be observed next to the ventricular lumen, and simultaneously migration of cells from the ventricular matrix layer begins to diminish. Rearrangement and spread of the cells is from then on a secondary process persisting into adult stages. No other cytoarchitectural changes of importance were noted in the ventricular wall however.

Migration commences at different times and takes place at different rates in the various migration areas. As described previously (BERGQUIST, 1952 c) the first migration occurs in *a.tub.post.* at the 8-day stage. At the next stage the migration has spread to the adjacent *a.c.hyp.* and *a.f.l.m.* All these migration areas border on plica encephali ventralis.

In most areas only a single cell migration takes place (*migr I*). Occasionally the migrated cells form diffuse groups which never become completely demarcated from the cell collections adjoining the ventricular surface.

Another type of migration takes place from *a.int.hyp.* whose cell groups within the wall become clearly demarcated from cells situated interiorly. All cells are derived from *migr I*. In this paper the former cell groups in the lateral ventricular wall are designated

VOL. 34 1953

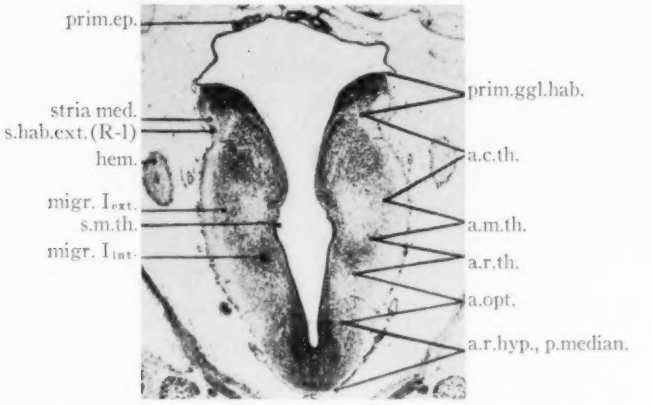


Fig. 4 a. *Lepidochelys olivacea*—21 day-stage (16 mm). Cross section in the rostral part of diencephalon. Magnification × 20.

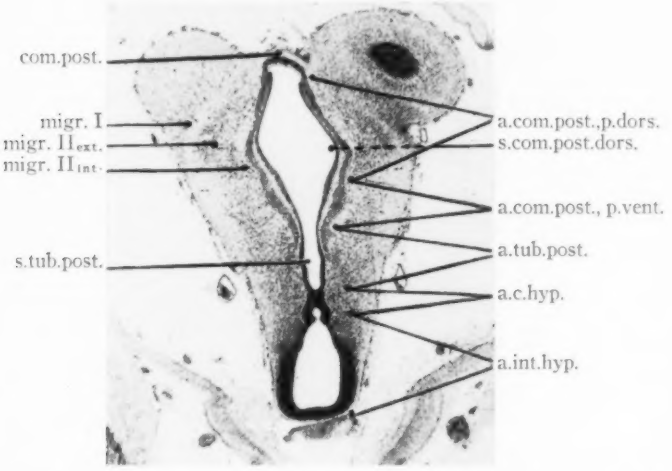


Fig. 4 b. *Lepidochelys olivacea*—21 day-stage (16 mm). Cross section in the caudal part of diencephalon. Magnification × 23.

migr $I_{ext.}$ and the latter *migr* $I_{int.}$. Fig. 6 illustrates such a migration from *a.int.hyp.* Additional information has been given by KÄLLÉN (1951 c) who in principle has unravelled the problem of these formative processes. By the 8-day stage cells from stratum matricis (*strat.matr.*) begin to invade stratum zonale (*strat.zon.*). This migration is continuing in the 11-day stage and has increased considerably in the 14—17 days stages. Not until the 21-day stage, when proliferation seems to have stopped, does this first migration layer (*migr I*) separate entirely from the ependymal layer at the ventricular lumen. At this juncture the layer begins to split into a lateral (*migr* $I_{ext.}$) and a medial (*migr* $I_{int.}$) portion, the separation being complete by the 26-day stage.

In *a.m.th. migr I* subdivides into three layers outside one another. They are here called *migr* $I_{ext.}$ (farthest out), *migr* $I_{med.}$ and *migr* $I_{int.}$ (closest in).

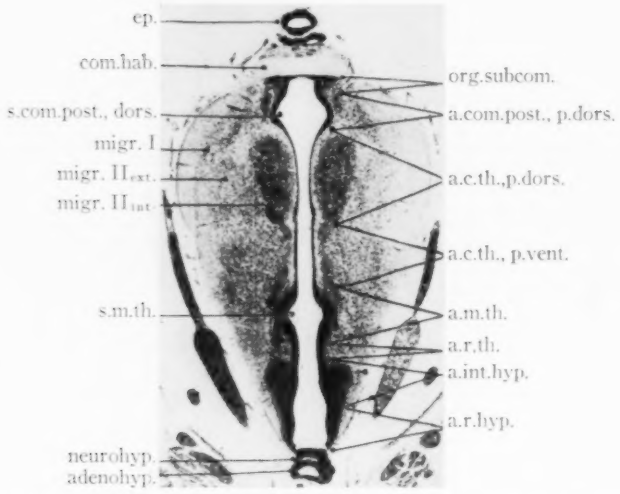
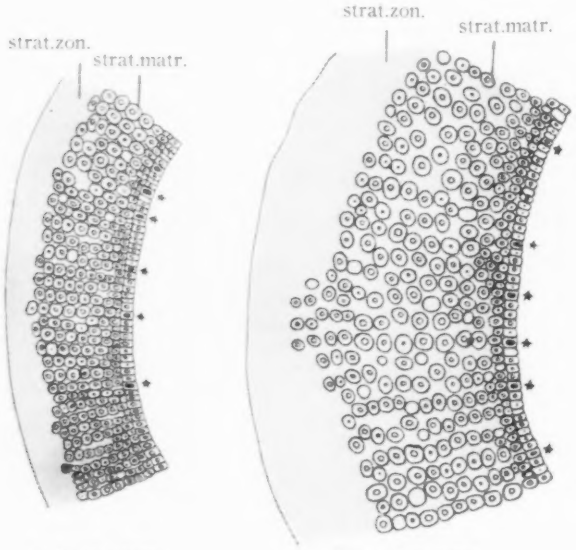


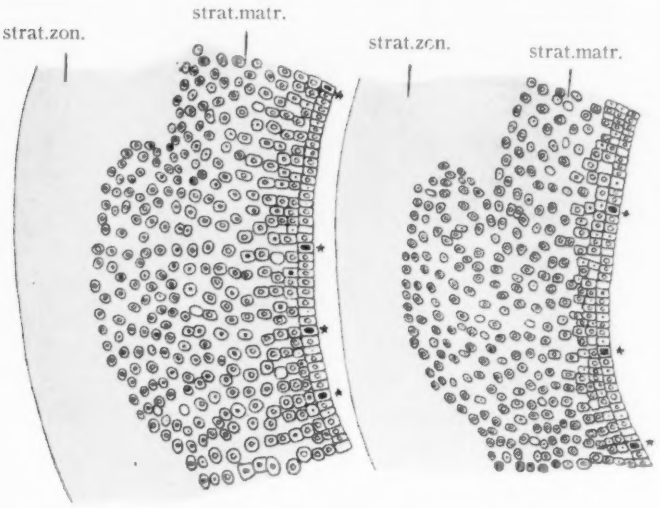
Fig. 5. *Lepidochelys olivacea*—26 day-stage (29 mm). Cross section in the middle part of diencephalon. Magnification × 20.



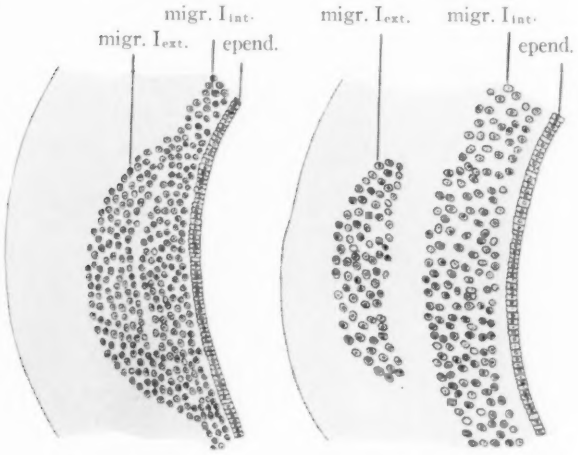
A. 8-day stage. B. 11-day stage.

Fig. 6. *Lepidochelys olivacea*—Schematic illustrations of the development of a cell migration from area intermedia hypothalami. Six stages A—F, are marked. They show the arrangement of the cells in cross-sections of the embryonic brain of the different stages. Stages A is a resting phase and the first migration (migr I) has not yet started. In stage B—D a first migration takes place and in stage E and F the migrated cells are separating from the ventricular gray (strat. matr.), which again is dormant. The migrated part is designated migr $I_{ext.}$ and the other cell portion migr $I_{int.}$ Migr $I_{int.}$ in stage E and F has separated from the ependymal layer (epend.) Cells in mitotic stages are marked by an asterisk. In stage E and F there are no such mitotic cells.

VOL. 34 1953



C. 14-day stage. D. 17-day stage.



E. 21-day stage. F. 26-day stage.

A second migration wave (*migr II*) occurs in only two areas, viz. in the dorsally fused portions of *a.c.th.* and *a.com.post.* Such a process has schematically been demonstrated by BERGQUIST & KÄLLÉN (1953 c, fig. 6). In both areas *migr II* splits into a lateral part, *migr* $II_{ext.}$, and a medial part, *migr* $II_{int.}$.

HYPOTHALAMUS

Morphologically *a.opt.* has divided into a larger rostral portion (*a.opt., p.rost.*) and a smaller caudal portion (*a.opt., p.caud.*). An unpaired nuclear area situated medially in *a.opt., p.rost.* (fig. 7 c and d), bulges out rostral to and around recessus praeopticus, and its lateral pockets. The cell group is in this paper called nucleus opticus rostralis, pars mediana

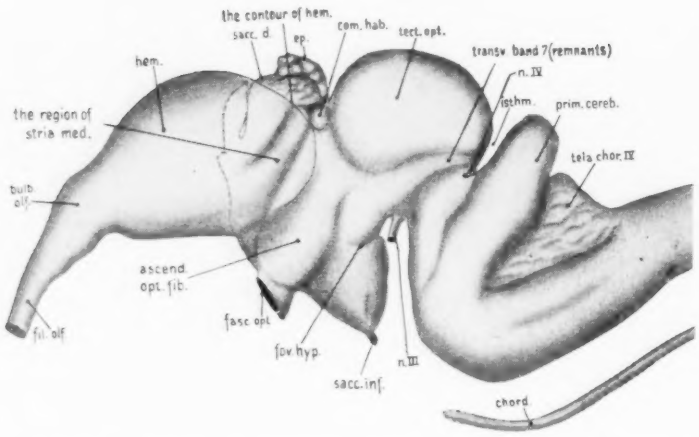


Fig. 7 a. *Lepidochelys olivacea*—28 day-stage (31 mm). Graph.e.l. Magnification × 15. The caudal part of the left hemisphere is marked with a contour line.

(nc.opt.rost., p. median.). On either side of the optic chiasma colomn it continues caudad. In the literature the whole collection of cells is usually called the preoptic nuclear area. Its median portion can be distinguished as far back as the 26-day stage. This median region is not marked off clearly from other portions of the cellular structure. RENDAHL called the entire region in *Gallus* and reptiles 'Kern i.m. und i.l.'; HUBER & CROSBY (1926), in *Alligator*, nucleus periventricularis preopticus etc.; KUROTSU (1935), in certain reptiles and avians, nucleus magnocellularis periventricularis; KUHLENBECK (1937), in *Gallus* and some reptiles, nucleus praeopticus paraventricularis; and ARIËNS KAPPERS (1942), in *Crotalus horridus* and other reptiles, nucleus periventricularis magno- et parvocellularis. In *Columba livia*, WINGSTRAND called part of the region 'the median preoptic nucleus' by which he referred to the septate ridge between the preoptic recesses on either side (cf. Wingstrand's fig. 129 B). The fibre connections in this region as well as in the rest of the hypothalamus are described in Wingstrand's paper, p. 208 ff.

A.opt., p.caud. gives origin to the supraoptic nucleus which is not very distinctly demarcated and whose cells tend to spread in a number of directions. In the pigeon it is composed of 'exclusively neurosecretory cells of the magnocellular type, whereas other parts also contain smaller non-secretory cells', (WINGSTRAND). By the term nucleus supraopticus (fig. 7 c and d) the present author refers to a nucleus apparently in part corresponding to Rendahl's 'Kern k1 und kl1' and the dorsal part of 'Kern a'. It could, according to Wingstrand, perhaps be identical with HUBER & CROSBY's (1929) nucleus magnocellularis interstitialis, and to KUHLENBECK's (1934) nucleus supraopticus. Wingstrand has let me study his *Tropidonotus natrix* series in which he observed a well demarcated and heavily stained nucleus supraopticus. I have been able to confirm this finding by observations in other *Tropidonotus* series.

A supraoptic nucleus in *Chamaeleon* is illustrated in fig. 3 of SHANKLIN's (1930) paper, but no such nucleus is described in the text. Even though it was diffuse, I have found the nucleus in *Chamaeleon* series from the Tornblad-Institute. Its position corresponded to that in Shanklin's illustration.

Another medially situated cell group is found in the caudal part of the optic chiasma beam constituting the rostromedian margin of *a.r.hyp.* It lies around the postoptic recess.

VOL. 34 1953

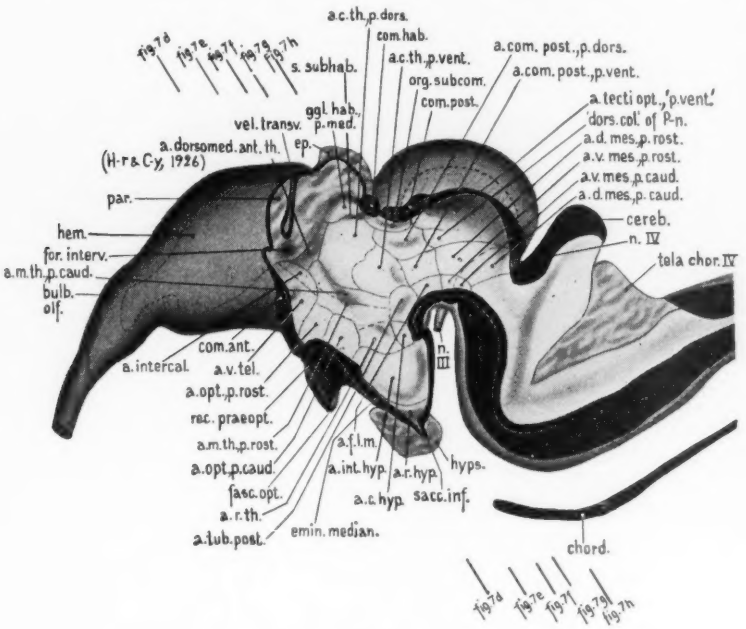


Fig. 7 b. *Lepidochelys olivacea*—28 day-stage (31 mm). Graph.i*. Magnification × 15.

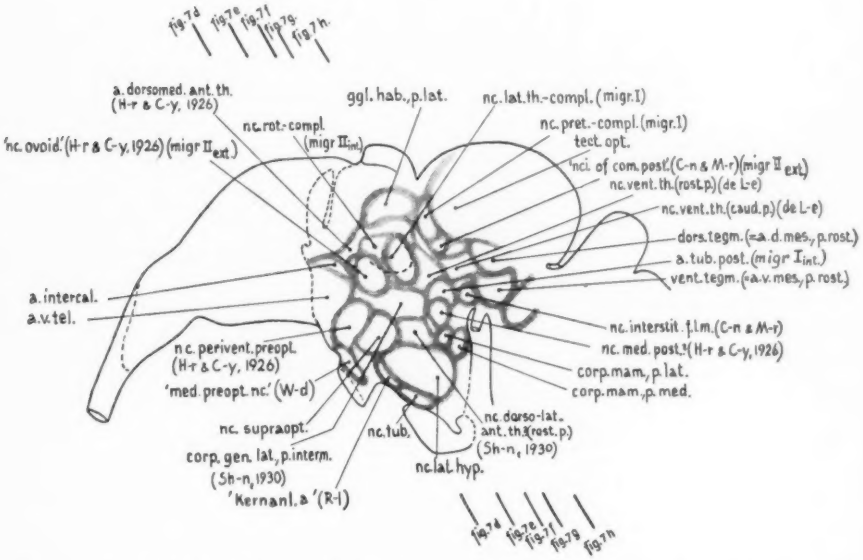


fig.7d
fig.7e
fig.7f
fig.7g
fig.7h
a. dorsomed. ant. th. (H-r & C-y, 1926)
ggl. hab.,p.lat.
nc. lat. th.-compl. (migr. I)
nc. pret.-compl. (migr. I)
tect. opt.
nc. rot.-compl. (migr II int.)
'nc. ovoid.' (H-r & C-y, 1926) (migr II ext.)
'nci. of com. post.' (C-n & M-r) (migr II ext.)
nc. vent. th. (rost.p.) (de L-e)
nc. vent. th. (caud.p.) (de L-e)
dors. tegm. (=a.d. mes., p.rost.)
a. tub. post. (migr I int.)
vent. tegm. (=a.v. mes., p.rost.)
a. intercal.
a.v. tel.
nc. interstit. f.l.m. (C-n & M-r)
nc. med. post.? (H-r & C-y, 1926)
nc. perivent. preopl. (H-r & C-y, 1926)
'med. preopt. nc.' (W-d)
corp. mam., p.lat.
corp. mam., p.med.
nc. supraopt.
nc. tub.
nc. dorso-lat.-ant. th. (rost.p.) (Sh-n, 1930)
corp. gen. lat., p.interm. (Sh-n, 1930)
nc. lat. hyp.
'Kernanl. a' (R-l)

Fig. 7 c. *Lepidochelys olivacea*—28 day-stage (31 mm). Graph.nuclei. Magnification × 15. The migration cell clusters are seen in lateral projection.

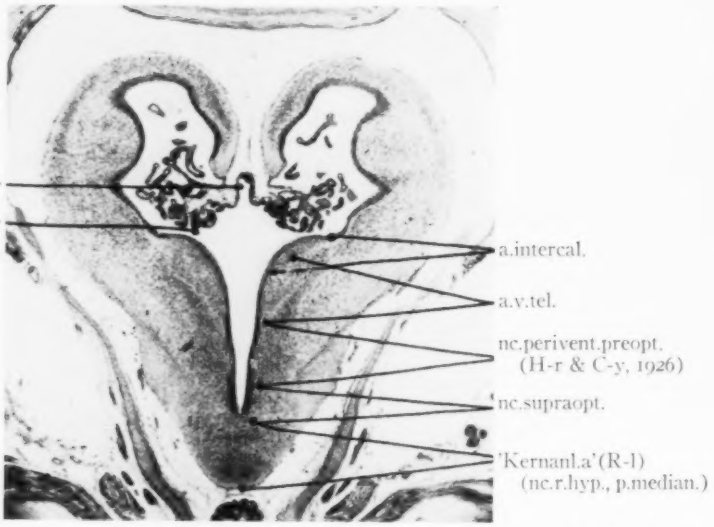


Fig. 7 d. *Lepidochelys olivacea*—28 day-stage (31 mm). Cross section, marked in the fig. 7 a—c. Magnification × 21.

As in the 4-day *Gallus* stage (RENDAHL), the cell group is concentrated to the region caudal to the chiasma at the 16-day stage. During later ontogeny it progresses caudad into the hypothalamus on both sides, in conformity with the rostro-median part of the *nc.opt.rost. p.median*. This median group of closely packed cells is a parallel to the ventral part of Rendahl's '*Kernanlage a*' and probably his '*Kernanlage a*$_1$', RENDAHL has not found such a 'nucleus a' in *Iguana*, but he has found it in very young *Tropidonotus*. In Alligator HUBER & CROSBY (1926) found a nucleus anterior hypothalami, which may correspond to this 'nucleus a'. Because this cell group recently has attracted special, both morphological and physiological, interest, I propose that it should be named, for example: nucleus rostralis hypothalami, pars mediana (*nc.r.hyp., p.median.*). In the *Lepidochelys*-series it can be distinguished from the 17-day stage (fig. 4 a, 7 c and d).

A cell group develops in the juxta-hypophysial portion of *a.r.hyp.* RENDAHL called it 'Kern m', and the ventral part of it seems identical to HUBER & CROSBY'S (1926) and SHANKLIN'S (1930) nucleus ventralis hypothalami. In birds Wingstrand called this portion of 'Kern m' nucleus tuberis, which seems a most appropriate name in view of its position in the "tuber cinereum" near the eminentia mediana. See *nc.tub.* fig. 7 c.

As early as at the 14-day stage *a.int.hyp.* undergoes rapid expansion and soon fills the greater part of the hypothalamus (fig. 2 b and d). During subsequent ontogeny this expansion becomes even more marked, as the illustrated reconstruction of the 28-day stage is intended to show in fig. 7 b.

In *a.int.hyp.* one can distinguish a medial (periventricular) and a lateral nuclear area. The two nuclei are named in conformity with the terminology used by ARIËNS KAPPERS, HUBER & CROSBY. The latter is called nucleus lateralis hypothalami (*nc.lat.hyp.*) and develop from *migr* $I_{ext.}$. It is illustrated in fig. 7 c, e and f. The former is called nucleus periventricularis hypothalami (*nc.perivent.hyp.*) and derives from *migr* $I_{int.}$ (fig. 7 f).

RENDAHL used the letters k and kl$_2$ to designate nuclear groups which apparently are derived from *a.int.hyp.*, whereas HUBER & CROSBY (1926) spoke of nuclei anterior,

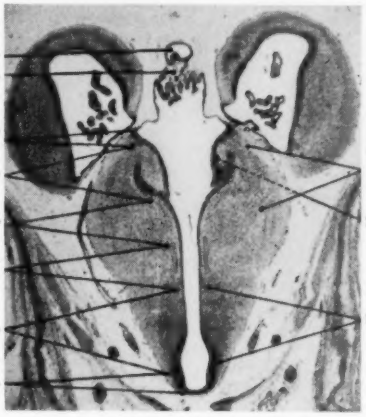


Fig. 7 e. *Lepidochelys olivacea*—28 day-stage (31 mm). Cross section, marked in the fig. 7 a—c. Magnification × 16.

OL.
34
953

periventricularis et lateralis hypothalami. CAIRNEY mentioned nucleus periventricularis hypothalami. Similar cell groups in *Lacerta muralis* have been described by DIEPEN and in *Chamaeleon* by SHANKLIN (1930).

The mammillary region is considered a part of the hypothalamus. Studying the migration of cells in the dorsal part of the hypothalamus in the *Lepidochelys* series, one finds at the 17-day stage a caudalmost part of *a.int.hyp.* (fig. 3) giving origin to a projecting cell mass which in stage 28-day is called corpus mammillare, pars medialis (*corp.mam., p.med.*). Just above this region, cells are establishing themselves around the recess in *a.c.hyp.* (fig. 3) where they later in the series form a lateral group here called corpus mammillare, pars lateralis (*corp.mam., p.lat.*) (fig. 7 c). RENDAHL used the terms nucleus mammillaris lateralis and nucleus mammillaris medialis dorsalis et ventralis in Varanus, Alligator, Gallus etc. DIEPEN (1943) would have them be cellulae mammillaria or cellulae basilaterales, or perhaps nucleus arcuatus. And while WINGSTRAND's nucleus mammillaris seems to correspond better with my caudal part of *nc.int.hyp.*, his nucleus subdecussationis appears to be a part of my *corp.mam., p.lat.*

EPITHALAMUS AND THALAMUS

The primordial ganglion habenulae has divided already by the 26-day stage. Here its lateral portion is called ganglion habenulae, pars lateralis (*ggl.hab., p.lat.*) and its medial portion ganglion habenulae, pars medialis (*ggl.hab., p.med.*) (*ggl.hab.* see fig. 7 b, c, f, g and h). Ganglion habenulae grows in a dorsocaudal direction above commissura habenularum (*com.hab.*; fig. 7 h). In early stages, e.g. the 14-day stage, the rostral part of the region is not clearly demarcated from the stria medullaris region. At the 28-day stage the region apparently corresponds to HUBER & CROSBY's (1926) area dorsomedialis anterior thalami. See fig. 7 b, c and e. Ganglion habenulae is wholly laid down during migr I. On the ventricular surface its ventral boundary is at later stages, e.g. the 28-day stage, marked by a furrow, sulcus subhabenularis (fig. 7 b). At the 20-day stage the forebrain bundles projects ventrolaterad into the rostral part of *a.r.th.* which later contracts and is squeezed caudad. And at the 28-day stage (fig. 7 b) *a.r.th.* is no longer in contact with the aforementioned tel-diencephalic intercalated area. This intercalated area will also be discussed at length in a forthcoming paper on the diencephalic nuclei in the entire vertebrate series.

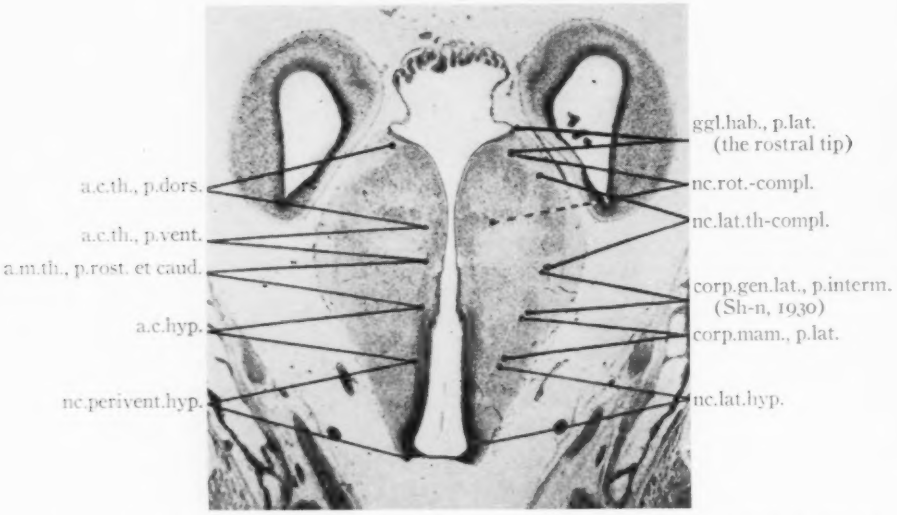
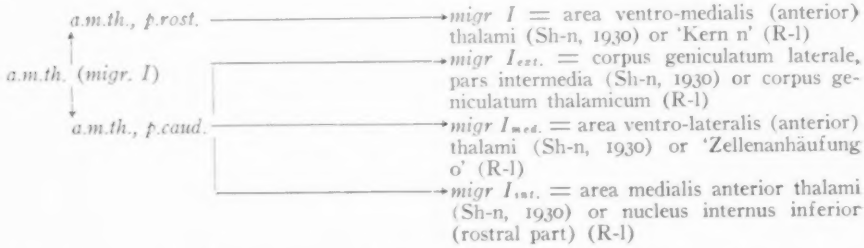


Fig. 7 f. *Lepidochelys olivacea*—28 day-stage (31 mm). Cross section, marked in the fig. 7 a—c. Magnification × 21.

A.r.th. (fig. 7 b, c and e) probably gives origin to Rendahl's 'Kern g' and his 'Kern h', but in the *Lepidochelys* 28-day stage such a nuclear subdivision cannot be observed. The cells instead form a rather diffuse aggregation which is well demarcated from surrounding areas. Very likely HUBER & CROSBY's (1926) area ventromedialis and this diffuse aggregation are identical. The region seems to correspond to the rostral part of SHANKLIN's (1930) nucleus dorso-lateralis anterior thalami and to KUHLENBECK's (1931) nucleus entopeduncularis.

The proliferation sulcus, *s.m.th.* which in early ontogeny is characteristic of *a.m.th.*, has in its middle by the 22-day stage, after mitotic activity has ceased, mainly the function of a demarcation sulcus between *a.m.th.* and *a.c.th.* A considerable number of cells have migrated from the *a.m.th.* In *Lepidochelys* only a single migration layer (*migr I*) has developed in *a.m.th.* It has, as mentioned, split into three layers, at the same time morphologically separating into a rostral part (*a.m.th., p.rost.*) and a caudal part (*a.m.th., p.caud.*). In the below tabulation SHANKLIN's (1930) and RENDAHL's terminology are juxtaposed with my own.


a.m.th., p.rost.
migr I = area ventro-medialis (anterior) thalami (Sh-n, 1930) or 'Kern n' (R-l)
migr I ext. = corpus geniculatum laterale, pars intermedia (Sh-n, 1930) or corpus geniculatum thalamicum (R-l)
a.m.th. (migr. I)
a.m.th., p.caud.
migr I med. = area ventro-lateralis (anterior) thalami (Sh-n, 1930) or 'Zellenanhäufung o' (R-l)
migr I int. = area medialis anterior thalami (Sh-n, 1930) or nucleus internus inferior (rostral part) (R-l)

Migr I ext. is also probably the same as HUBER & CROSBY's (1926) nucleus diagonalis.

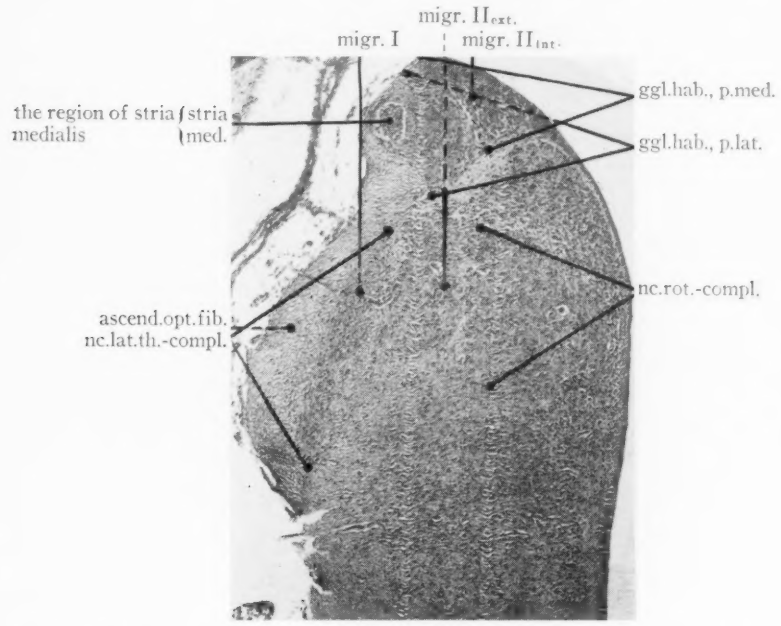


Fig. 7 g. *Lepidochelys olivacea*—28 day-stage (31 mm). Cross section, marked in the fig. 7 a—c. Magnification × 53. The section is crossed by two vertical microtome tracks.

The shrub-like cell migration in *a.tub.post.* has expanded laterally (fig. 4 b). It conforms to the ventral part of RENDAHL's nucleus superficialis magnocellularis and probably nucleus ectomammillare and perhaps to HUBER & CROSBY's (1926) nucleus medialis posterior thalami.

Considerable changes have taken place in *a.c.th., p.dors.* Thus, a medially situated nucleus rotundus complex (*nc.rot.-compl.*; fig. 7 c, f and g) has developed in *migr II$_{int.}$*. Latero-rostrally to it a cell cluster of *migr II$_{ext.}$* seems on the whole homologous with nucleus ovoideus of HUBER & CROSBY (1926) and corpus geniculatum laterale, pars dorsalis of CAIRNEY. ARIËNS KAPPERS, HUBER & CROSBY use the terms nucleus dorsolateralis anterior and area triangularis. See '*nc.ovoid.*' (H-r & C-y, 1926) in fig. 7 c and e. Latero-caudally of the nucleus rotundus-complex and medially of the ascending optic bundles there lies a group of scattered cells belonging to *migr I.* I have called it nucleus lateralis thalami-complex (*nc.lat.th.-compl.*; fig. 7 c, f and g). In *Sphenodon* (CAIRNEY) it seems partly homologous with nucleus dorsolateralis anterior. CROSBY (1917) distinguished in its lateral portion a 'pulvinar' cell area. In a forthcoming survey of diencephalic nuclei in vertebrates I hope to return to this interesting observation. *A.c.th., p.vent.* may be related to the rostral part of nucleus ventralis thalami in *Varanus* (DE LANGE) [*nc.vent.th.* (*rost.p.*) (de L-e); fig. 7 c] and possibly with nucleus interstriaticus in *Gallus* and reptiles (RENDAHL). The area corresponds to ARIËNS KAPPERS, HUBER & CROSBY's nucleus tractus tectothalami cruciati, area ventrolateralis and area ventromedialis, nucleus entopeduncularis, nucleus decussationis supraopticus dorsalis and nucleus microcellularis.

The table of synonyms reproduced below is an attempt to systematize the various names given to different nuclei in this part of the brain by RENDAHL, HUBER & CROSBY (1926) and the present author.

Rendahl (1924)	Huber & Crosby (1926)	Bergquist (*a.c.th., p.dors.*)
nucleus subrotundus nucleus rotundus thalami	area triangularis	*migr I* = nucleus lateralis thalami complex (*nc.lat.th.-compl.*)
column of cells superficially in the ventricular wall, designated *k.d.o.S.*, etc.	'geniculatum pretectale' 'corpus geniculatum laterale'	
nucleus rotundus (thalami) Kern A_3	nucleus ovoideus	*migr* $II_{ext.}$ = 'nucleus ovoideus' ('*nc.ovoid*'.) (H-r & C-y, 1926)
nucleus internus superior	nucleus dorsomedialis anterior thalami	
nucleus internus inferior (caudal part) Kern A_2 Kern B	nucleus subhabenularis nucleus medialis anterior (thalami) nucleus medialis posterior thalami nucleus posterodorsalis nucleus rotundus (cf. Ariëns Kappers, Huber & Crosby)	*mtgr* $II_{int.}$ = nucleus rotundus-complex (*nc.rot.-compl.*)

It seems reasonable to suppose that this area also should be regarded as including nuclei reunientes in the massa intermedia, which is indicated by studies on *Chrysemys marginata* (*juv.*) and other species, for instance on Vipera and Lacerta.

SYNENCEPHALON

A certain degree of cell migration has taken place in the superior part of *a.com.post.* where organon subcommissurale is situated. In the rostral part of the area it might be possible to find a corollary to nucleus angularis subhabenularis in *Alligator* (Huber & Crosby, 1926).

In *a.com.post., p.dors.* (fig. 7 h) a wave of cells have migrated into the region separating the diencephalon from the mesencephalon. Here follows a tabulation of Curwen & Miller's (1939) results of and the present author's.

Curwen & Miller	Bergquist (*a.com.post., p.dors.*)
nucleus lentiformis etc. nucleus pretectalis etc. nucleus commissuralis posterior(?)	*migr I* = nucleus pretectalis-complex (*nc.pret.-compl.*)
nuclei posterodorsalis, dorsolateralis posterior and the three nuclei of the posterior commissure	*migr* $II_{ext.}$ = 'nuclei of the posterior commissure' ['*nci.of com. post.*' (C-n & M-r)]
nuclei interstitiales of the posterior commissure paracentral gray	*migr* $II_{int.}$ = nuclei grisei paracentralis (*nci.gr.parac.*)

At the 18-day stage the two parts of *migr II* remain incompletely divided, but as from the 19-day stage of the embryonic series division is complete (see in 21-day stage fig. 4 b). As early as the 19-day stage my nucleus pretectalis-complex is established distally in the ventricular wall. At older stages tectum opticum has grown over and covers this complex

VOL 34 195

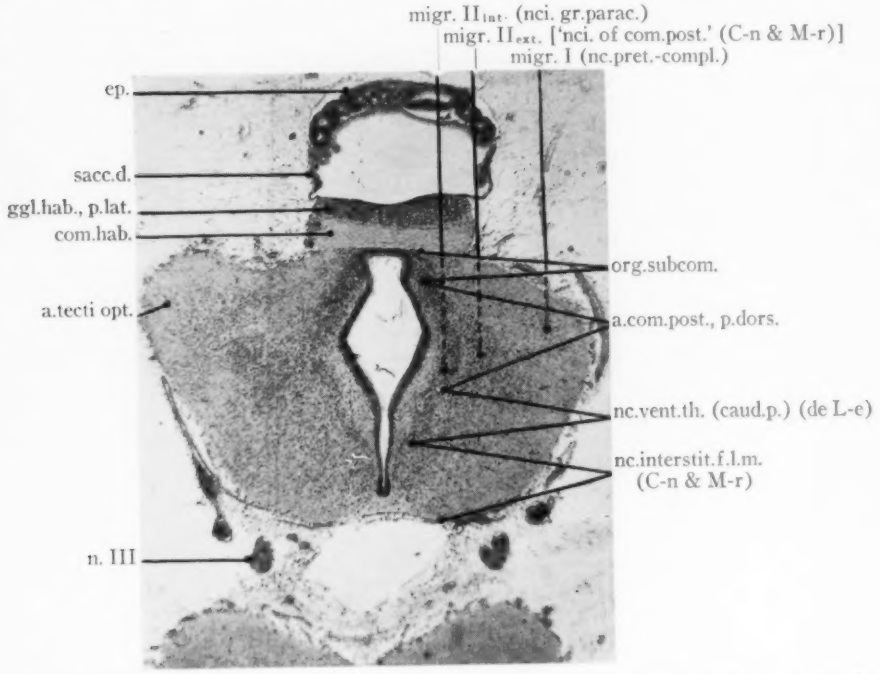


Fig. 7 h. *Lepidochelys olivacea*—28 day-stage (31 mm). Cross section, marked in the fig. 7 a—c. Magnification × 30.

(fig. 7 h). The corresponding cell group in *Draco volans* DE LANGE called nucleus lentiformis.

In birds and reptiles RENDAHL has found nucleus dorsocaudalis laterally from the organon subcommissurale. RENDAHL's 'hintere Kernplatte', his nucleus praetectalis and nucleus superficialis synencephali, as other nuclei mentioned by him are developed from *a.com.post., p.dors.* in its *migr I.* RENDAHL's nucleus superficialis synencephali is by EDINGER in *Chamaeleon* called corpus geniculatum mediale. The nuclei by me termed *nci.grisei* paracentralis are identical to part of RENDAHL's stratum cellulare internum et ependymale. CAIRNEY called it among other things nucleus lentiformis mesencephali. SHANKLIN (1930) distinguished nucleus lentiformis mesencephali, nucleus lentiformis thalami, nucleus pretectalis, nucleus geniculo-pretectalis and nucleus postero-centralis (thalami). A large number of cells belonging to *migr II$_{ext.}$* have migrated, although they are poorly demarcated from *migr II$_{int.}$* in the medial region (fig. 7 h). I have given the former region the inclusive name 'nuclei of the posterior commissure' (*'nci. of com.post.'*) (C-n & M-r) and the latter cell clusters are called nuclei grisei paracentralis (*nci.gr.parac.*).

a.com.post., p.vent. is not so well demarcated from *a.com.post., p.dors.* in older stages (fig. 7 h). It apparently is the equivalent of the caudal part of the nucleus ventralis thalami in *Varanus* (DE LANGE).

Migrating cells in *a.f.l.m.* form a diffuse aggregation closely related to similar cells from both *a.tub.post.* and *a.v.mes., p.rost.* in the rostro-ventral part of tegmentum. Together with *a.f.l.m.* the latter area corresponds to the ventral portion of RENDAHL's nucleus fasci-

culi longitudinalis, termed by him *nc.f.d₂.* and to nucleus interstitialis *f.l.m.* + nucleus interstitialis tegmenti in CURWEN & MILLER.

Remnants of transversal band 7 persist as far up as in the tectum opticum region at the 28-day stage (fig. 7a). Further data on the development of mesencephalon in Mus will be given in BENGMARK, HUGOSSON & KÄLLÉN.

For supplementation and control of the *Lepidochelys* series an investigation was made of embryonic *Chrysemys* series and some other reptilian series specified in the list of materials on pp. 184 foll. Embryonic series of *Columba livia* was used to provide a basis for comparison with RENDAHL's investigation of *Gallus* and with WINGSTRAND's of hypothalamic relationships in birds in general. In the below appropriate parts of the *Chrysemys* series will be described and contrasted with the corresponding *Lepidochelys* structures.

Chrysemys marginata—1.64 mm (head length)

By this stage the synencephalic area is somewhat elongated, and primordia of the paraphysis and epiphysis have already developed. Most of the hypothalamic, thalamic and synencephalic migration areas occurring in the embryonic vertebrate brain have appeared. Neither external nor ventricular sulci have yet vanished completely. Stratum zonale persists in but a few areas as a very thin lamina.

Chrysemys marginata—2.72 mm (head length)

Invagination of the sulcus hemisphaericus (*s.hem.*) has begun caudally of the hemisphere primordia, and a short fovea hypothalmica (*fov.hyp.*) is visible as well.

The migration areas are scarcely more developed than at the preceding stage. The following proliferative sulci can be distinguished: sulcus medialis thalami, sulcus opticus, sulcus intermedius hypothalami, sulcus caudalis hypothalami and sulcus fasciculi longitudinalis medialis (*s.f.l.m.*). Primordia of the ansulate and posterior commissures as well as of the optic chiasma system have developed. At most places stratum zonale can be seen in the most lateral part of the ventricular wall.

Chrysemys marginata—2.19 mm (head length)

Externally the prospective dorsal sac has established itself, and cells are beginning to enter stratum zonale from migration areas bordering against plica encephali ventralis, e.g. from *a.tub.post.* and *a.f.l.m.*

Chrysemys marginata—3.59 mm (head length)

As from this stage all the vertebrate series' normal migration areas are developed and, in addition, some of them have subdivided: *a.m.th., p.rost.*; *a.m.th., p.caud.*; *a.c.th., p.dors.*; *a.c.th., p.vent.*; *a.com.post., p.dors.* and *a.com.post., p.vent.* And the caudal portion of *a. int.hyp.* has grown. The primordial ganglion habenulae is established in the dorsal portion of *a.c.th.* In the mesencephalic region one can distinguish the usual tegmental cell columns and in *a.tecti.opt.* PALMGREN's "dorsal cell column". Cell migration has continued and now affects almost all migration areas.

Chrysemys marginata—4.4 mm (head length), 11 mm (carapace length) and a stage designated *juv.* (fig. 8)

As from this stage an intercalated area (*a.intercal.*) is present between *a.d.tel.* and *a.r.th.* The hypothalamus is becoming more and more saccular and its narrow end (saccus in-

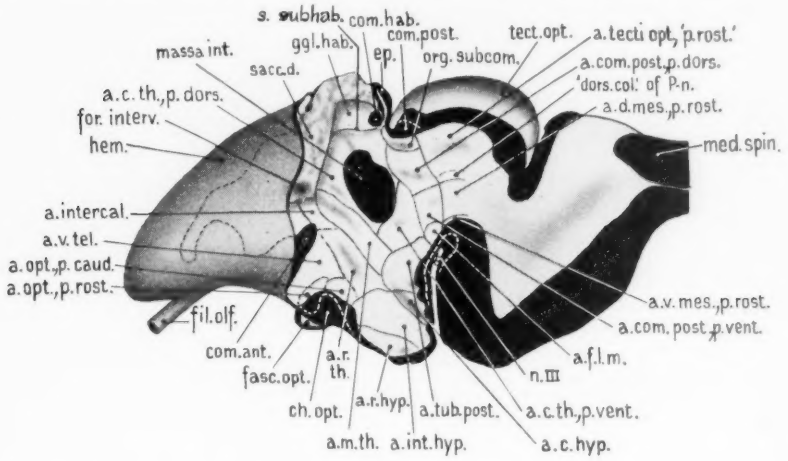


Fig. 8. *Chrysemys marginata*—juv.-stage. Graph.i. Magnification × 17.

fundibuli) is directed caudad. A subcommissural organ is present and the anterior and habenular commissures are established.

Medially continued cell migration has established the *migr I* layer in *a.m.th.*, where groups of nuclei largely corresponding to those in *Lepidochelys* 28-day stage are apparent. There has developed in the dorsal part of *a.c.th.* already by 11-mm stage (*a.c.th., p.dors.*) a massa intermedia which forms a bridge to the contralateral aspect of the ventricular lumen (fig. 8). A number of cells visible in massa intermedia correspond to nuclei reunientes. Furthermore groups of nuclei resembling those in the *Lepidochelys* 28-day stage have emerged in *a.c.th.* and in *a.com.post., p. dors.*

Embryonic series of *Dermochelys, Trionyx, Alligator, Crocodilus, Chalcides, Vipera* and *Tropidonotus* displayed nothing remarkable in addition to the features described. Nevertheless, mature nuclei are not seldom rather variable as to shape and density. This applies, for example, to nucleus supraopticus.

IV. DISCUSSION

As the proliferation at the ventricular lumen is coming to an end, the medial thalamic sulcus (*s.m.th.*) is being displaced from the central to the extreme caudal portion of *a.m.th.*, so that the sulcus is marginal when the proliferation is over. Similar movements of other sulci have been observed previously by BERGQUIST (1932 and 1952 c), RUDEBECK (1945), and KÄLLÉN (1950, 1951 a and b). A marginal furrow corresponding to *s.m.th.* has been described by HERRICK (1933, 1948 etc.) under the name of sulcus diencephalicus medius, demarcating the 'dorsal' from the 'ventral thalamus'. Sulcus subhabenularis is in *Lepidochelys* on the contrary from the very beginning a marginal furrow separating ganglion habenulae from the remainder of *a.c.th., p.dors.* (fig. 7 b). Cf.

also the relation in *Chrysemys* (fig. 8). The HERRICK-school has stressed the significance of these marginal furrows because they are useful landmarks, separating various structures, in diencephalon including, the epithalamus, the dorsal thalamus, the ventral thalamus and the hypothalamus. But, as noted above, in younger stages these sulci lie in the middle of the migration areas. As the HERRICK-school as a rule has studied later embryonic stages, whereas we have investigated the cerebral tube's development at much earlier stages, it is really not so strange that our opinions are at odds on certain points (cf. BERGQUIST, 1952 c).

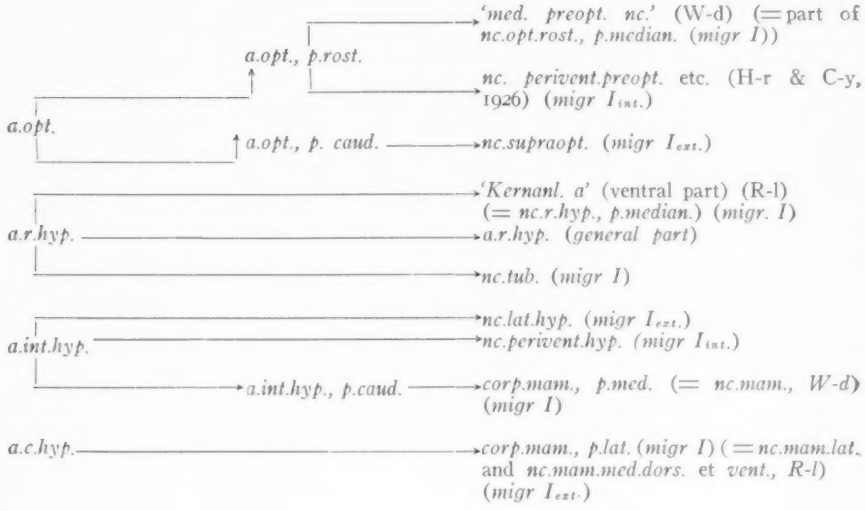
During early ontogenesis the ventricular gray undergoes no longitudinal structuration, but like the marginal furrows longitudinal banding becomes manifest in later embryonic stages. In the *Lepidochelys* 14-day stage, for example, the longitudinal phase is dominant in the ventral diencephalon, as is described on pp. 161 foll. of the present paper. KÄLLÉN and I have in our paper of 1953 c discussed the longitudinal columns that the HERRICK-school has made the subject of a long series of significant publications.

VOL.
34
1953

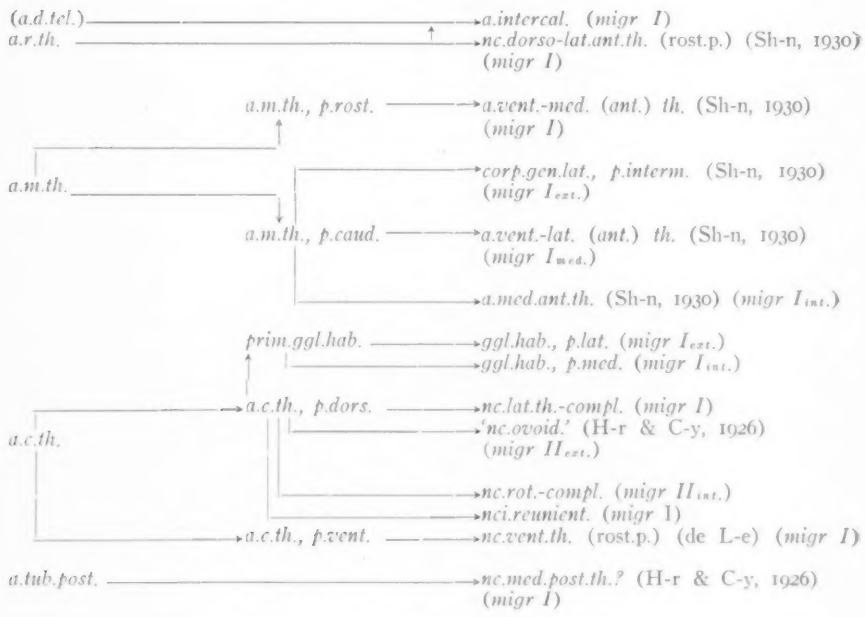
The cell migration peripherally in the brain is commented on pp. 165 foll. of this paper. It starts in *a.tub.post.*, continues in areas bordering on the ventral encephalic fold and ultimately involves also the remaining diencephalic and mesencephalic migration areas studied. This primary migration wave (*migr I*), however, gives rise to rather different results in the various migration areas. Thus, in most areas it gives origin to one cell stratum only. But, on the other hand, while two cell layers (*migr* $I_{int.}$ and *migr* $I_{ext.}$) are established in *a.int.hyp.*, as many as three such layers (*migr* $I_{int.}$, *migr* $I_{med.}$ and *migr* $I_{ext.}$) develop in *a.m.th.* A secondary migration wave (*migr II*) enters only two migration areas, namely the dorsal portions of *a.c.th.* and *a.com.post.* It lays down two layers (*migr* $II_{int.}$ and *migr* $II_{ext.}$) medially of the undivided *migr I* layer. When proliferation is over, i.e. as from the Lepidochelys 20-days stage, nuclear formation enters its ultimate phase.

Like FEREMUTSCH (1949) and other authors, I have analyzed larger nuclear units only. Their mode of development is decisive for homologization with other animals' nuclei, and thus for the appropriate terminology. Migration areas and layers were made the foundation for homology. Nuclei discussed in this paper were not set in closer relation to those in mammals and man. For, as mentioned, this paper presents merely one of a series of investigations having the common aim of providing an analysis of the homologous diencephalic nuclei in vertebrates in general. All the migration areas found throughout the vertebrate series by BERGQUIST or KÄLLÉN or both in collaboration, were also observed in the *Lepidochelys*, *Chrysemys* and in other series presented here. The below is a scheme illustrating the ontogenesis of nuclei in *Lepidochelys olivacea:*

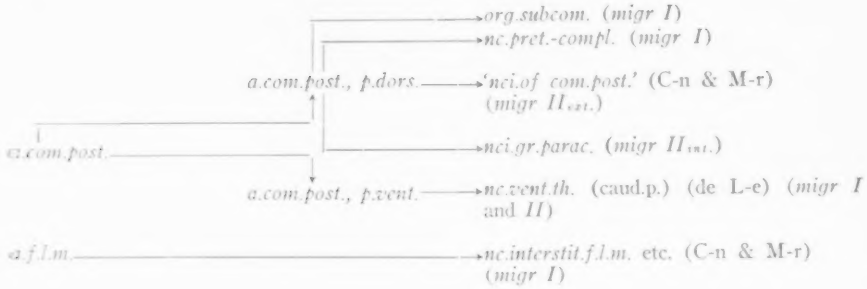
HYPOTHALAMUS


'med. preopt. nc.' (W-d) (=part of nc.opt.rost., p.median. (migr I))
a.opt., p.rost.
nc. perivent.preopt. etc. (H-r & C-y, 1926) (migr I int.)
a.opt.
a.opt., p. caud.
nc.supraopt. (migr I ext.)
'Kernanl. a' (ventral part) (R-l) (= nc.r.hyp., p.median.) (migr. I)
a.r.hyp.
a.r.hyp. (general part)
nc.tub. (migr I)
nc.lat.hyp. (migr I ext.)
a.int.hyp.
nc.perivent.hyp. (migr I int.)
a.int.hyp., p.caud.
corp.mam., p.med. (= nc.mam., W-d) (migr I)
a.c.hyp.
corp.mam., p.lat. (migr I) (=nc.mam.lat. and nc.mam.med.dors. et vent., R-l) (migr I ext.)

EPITHALAMUS and THALAMUS



SYNENCEPHALON



The distribution and relations of nerve fibres in the diencephalon has been discussed among others by HUBER & CROSBY (1926) and CURWEN & MILLER, and also in the monograph by ARIËNS KAPPERS, HUBER & CROSBY (1936). The limiting interparencephalic zone in the 14-day stage has been described (RENDAHL) as a very marked demarcation between my *a.m.th.* and *a.c.th.* This comparatively cell-free area in ventricular gray will eventually be the site of development of a fibre fasciculus, the thalamo-mammillary tract. According to GILBERT (1935) and others 'zona limitans intrathalamica' in man separates 'the ventral and the dorsal thalamus'. In a similar position between *a.c.th.* and *a.com.post.* BERGQUIST (1932) in lower vertebrates observed the formation of the habenulo-peduncular tract (Meynert's bundle). This bundle could not be perceived in the available *Lepidochelys* cross-sections, because the borderline in question usually coincided with the direction of the cut. In adult animals such cell regions are often separated by 'laminae', which have been described in particular detail in mammals, but especially in man.

In a preceding paper BERGQUIST (1952 c) already observed that in *Lepidochelys* the longitudinal component crosses over transversal band 7 much later than more rostral transversal bands. By the 9-day stage *a.v.mes., p.caud.* is beginning to develop, and it is expanding rapidly in the 11-day and 12-day stages. But even at the 28-day stage remnants of transversal band 7 can be observed in the caudal portion of the tectum opticum.

V. SUMMARY

1. Diencephalic migration layers have been analyzed, chiefly in an embryonic series of *Lepidochelys olivacea*.

2. In the same material the development of diencephalic, nuclei has been studied; comparisons have been made with some other reptiles and birds. The results are given in tabular form on pp. 179 foll.

VOL. 34 1953

3. My nuclear analysis has been based on migration areas and migration layers. The areas in number and location conformed fully with previous observations in the corresponding regions of other vertebrates. In subsequent investigations I shall discuss the problems about the homologizations of the diencephalic nuclei throughout the vertebrate series.

4. The region in ventricular gray between *a.m.th.* and *a.c.th.* has been found to contain a fibre fasciculus, tractus thalamo-mammillaris. Tractus habenulopeduncularis in lower vertebrates has previously been found in the region separating *a.c.th.* and *a.com.post.* (BERGQUIST, 1932).

5. Remnants of transversal band 7 could be observed in the mesencephalon even at the 28-day stage, when nuclear development is almost complete rostrally. The dorsal portion of this band can be observed in the caudal part of tectum opticum. The longitudinal component crosses over the band much later than more rostral bands.

VI. ABBREVIATIONS[5]

* denotes that the illustration is reversed, side-to-side
a.c.hyp. area caudalis hypothalami
a.c.th. area caudalis thalami
a.c.th., p.dors area caudalis thalami, pars dorsalis
a.c.th., p.vent. area caudalis thalami, pars ventralis
a.com.post., p.dors. area commissurae posterioris, pars dorsalis
a.com.post., p.vent. area commissurae posterioris, pars ventralis
a.d.mes., p.caud. area dorsalis mesencephali, pars caudalis
a.d.mes., p.rost. area dorsalis mesencephali, pars rostralis
a.d.tel. area dorsalis telencephali
a.dorsomed.ant.th. (H-r & C-y, 1926) area dorsomedialis anterior thalami (HUBER & CROSBY, 1926)
a.f.l.m. area fasciculi longitudinalis medialis
a.int.hyp. area intermedia hypothalami
a.intercal. area intercalata (a boundary region between *a.d.tel.* and *a.r.th.*)
a.m.th. area medialis thalami
a.m.th., p.caud. area medialis thalami, pars caudalis
a.m.th., p.rost. area medialis thalami, pars rostralis
a.opt. area optica
a.opt., p.caud. area optica, pars caudalis
a.opt., p.rost. area optica, pars rostralis
a.r.hyp. area rostralis hypothalami
a.r.hyp., p.median. area rostralis hypothalami, pars mediana
a.r.th. area rostralis thalami
a.tecti.opt. area tecti optici
a.tecti.opt, 'p.rost.' area tecti optici, 'pars rostralis'[6]
a.tub.post. area tuberculi posterioris
a.v.mes., p.caud. area ventralis mesencephali, pars caudalis
a.v.mes., p.rost. area ventralis mesencephali, pars rostralis
a.v.tel. area ventralis telencephali
adenohyp. adenohypophysis
ascend.opt.fib. ascending optic fibers
bulb.olf. bulbus olfactorius

[5] Compare the more detailed list of abbreviations in BERGQUIST, 1952 b.

[6] Whether a. tecti opt. is divided into a rostral and a caudal part has not been established. 'Pars rostralis' is therefore put in quotation marks. The caudal part might be formed by the dorsal portion of the transversal band 7 (cf. BERGQUIST, 1952 c).

bursa R. bursa Rathkei
bursa Sces. bursa Scesselis
cereb. cerebellum
ch.opt. chiasma fasciculorum opticorum
chord. chorda dorsalis
com.ant. commissura anterior
com.hab. commissura habenularum
com.post. commissura posterior (caudalis)
con.opt. conus opticus
corp.gen.lat., p.interm. (Sh-n, 1930) corpus geniculatum laterale, pars intermedia and in part area ventromedialis (anterior) thalami (SHANKLIN, 1930)
corp.mam., p.lat. corpus mammillare, pars lateralis (= caudal part of *a.c.hyp.*)
corp.mam., p.med. corpus mammillare, pars medialis (= caudal part of *a.int.hyp.*)
'dors.col.' of P-n dorsal cell column of PALMGREN (1921)
dors.tegm. dorsal part of tegmentum
dr.graph.e.l.i. and nuclei draught and graphic reconstruction of externo-lateral and internal (ventricular) surface of the embryonic brain and cerebral nuclei
emin.median. eminentia mediana (WINGSTRAND, 1951)
ep. epiphysis cerebri
epend. stratum ependymale (= ependymal layer)
evag.hem. evaginatio hemisphaerica
fasc.opt. fasciculus opticus
fil.olf. fila olfactoria
flex.cer-spin. flexura cerebro-spinalis (= nuchal flexure)
for.interv. foramen interventriculare (= foramen of Monro)
fov.hyp. fovea hypothalamica
ggl. V ganglion trigemini
ggl. VII and VIII ganglion acustico-faciale
ggl.hab., p.lat. ganglion habenulae, pars lateralis
ggl.hab., p.med. ganglion habenulae, pars medialis
graph.e.l. graphic reconstructions of externo-lateral surface of the embryonic brain
*graph.e.l.** graphic reconstruction of externo-lateral surface of the embryonic brain, reversed
graph.i. graphic reconstruction of internal (ventricular) surface of the embryonic brain
*graph.i.** graphic reconstruction of internal (ventricular) surface of the embryonic brain, reversed
graph.nuclei graphic reconstruction of the cerebral nuclei
hem. hemisphere
hl. head length (see VII List of material in this paper)
hypoth. hypothalamus
hyps. hypophysis cerebri
isthm. isthmus rhombencephali
'Kernanl.a' (*R—l*) 'Kernanlage a' (ventral part) (RENDAHL, 1924) and possibly his 'Kernanlage a_1'
massa int. massa intermedia
'med.preopt.nc.' (*W-d*) median preoptic nucleus (WINGSTRAND, 1951) etc.
med.spin. medulla spinalis
migr I the first migration layer
migr $I_{ext.}$ the external part of migr I
migr $I_{int.}$ the internal part of migr I
migr II the second migration layer
migr $II_{ext.}$ the external part of migr II
migr $II_{int.}$ the internal part of migr II
n. III nervus oculomotorius
n. IV nervus trochlearis
nc.dorso-lat.ant.th. (Sh-r, 1930) nucleus dorso-lateralis anterior thalami (SHANKLIN, 1930)
nc.interstit.f.l.m. nucleus interstitialis f.l.m. and nucleus interstitialis tegmenti (CURWEN & MILLER, 1939)
nc.lat.hyp. nucleus lateralis hypothalami
nc.lat.th.-compl. nucleus lateralis thalami-complex
nc.med.post.? (H-r & C-y, 1926) nucleus medialis posterior? (HUBER & CROSBY, 1926)
'nc.ovoid.' (H-r & C-y) nucleus ovoideus (HUBER & CROSBY, 1926)
nc.perivent.hyp. nucleus periventricularis hypothalami etc.
nc.perivent.preopt. (H-r & C-y, 1926) nucleus periventricularis preopticus etc. (HUBER & CROSBY, 1926)
nc.pret.-compl. nucleus pretectalis-complex
nc.r.hyp., p.median. nucleus rostralis hypothalami, pars mediana

VOL. 34 1953

nc.rot.-compl. nucleus rotundus-complex
nc.supraopt. nucleus supraopticus
nc.tub. nucleus tuberis
nc.vent.th. (de L-e) nucleus ventralis thalami (DE LANGE, 1913)
nci.gr.parac. nuclei grisei paracentralis
'nci. of com.post.' (C-n & M-r) nuclei of the posterior commissure (CURWEN & MILLER, 1939)
neur VI—X neuromeres VI—X
opt.fib. optic fibers
org. subcom. organon subcommissurale
par. paraphysis
ped.opt. pedunculus opticus
prim.cereb. primordial cerebellum
prim.com.ans. primordial commissura ansulata
prim.com.cereb. primordial commissura cerebellaris
prim.com.post. primordial commissura posterioris (caudalis)
prim.ep. primordial epiphysis
prim.ggl.hab. primordial ganglion habenulae
prim.par. primordial paraphysis
prim.sacc.d. primordial saccus dorsalis
rec.c.hyp. recessus caudalis hypothalami
rec.praeopt. recessus praeopticus
s.c.th. sulcus caudalis thalami
s.c.th.vent. sulcus caudalis thalami, ventralis (in *a.c.th., p.vent.*)
s.com.post.dors. sulcus commissurae posterioris dorsalis (in *a.com.post., p.dors.*)
s.com.post.vent. sulcus commissurae posterioris ventralis (in *a.com.post., p.vent.*)
s.hem. sulcus hemisphaericus
s.int.hyp. sulcus intermedius hypothalami
s.m.th. sulcus medialis thalami (= sulcus diencephalicus medius, HERRICK, 1933 etc.; cf. BERGQUIST, 1952 c, footnote 2)
s.opt. sulcus opticus (= sulcus praeopticus)
s.r.hyp. sulcus rostralis hypothalami
s.hab.ext. (R—l) sulcus habenularis externus (RENDAHL, 1924)
s.subhab. sulcus subhabenularis
s.tub.post. sulcus tuberculi posterioris
sacc.d. saccus dorsalis
sacc.inf. saccus infundibuli
sin. VI—X sinuationes VI—X (= ventricular furrows in neuromeres VI—X)
strat.matr. stratum matricis
strat.zon. stratum zonale
stria med. stria medullaris
taen.th. taenia thalami
tect.opt. tectum opticum
tela chor. IV tela chorioidea ventriculi quarti
transv. band 7 transversal band 7 (BERGQUIST, 1952 c)
wax-pl.e.l. and i. wax-plate reconstruction of externo-lateral and internal (ventricular) surface of the embryonic brain
wax-pl.ventr.gr. wax-plate reconstruction of the ventricular gray
vel.transv. velum transversum
vent.tegm. ventral part of tegmentum
ves.aud. vesicula auditiva (= otic vesicle)
zona lim.interpar. (R-l) zona limitans interparencephalica (RENDAHL, 1924); = zona limitans intrathalamica, KUHLENBECK, 1930)

VII. LIST OF MATERIAL

ABBREVIATIONS:

sag. = sagittal; transv. = transversal; horiz. = horizontal; * denotes that the illustration is reversed. Sources: L = Tornblad-Institute for Comparative Embryology, Lund; S = Zootomical Institute, Stockholm; ZL = Zoological Institute, Lund.

Apart from the material listed below other series have been studied, but they have not been listed as they were of minor importance for this study.

Unless the contrary is stated the sections were stained with haematoxylin-eosin or by Azan's method. The right half of the embryonic brain has usually been reconstructed.

The length and the age of the embryos used cannot be looked upon as true measures of the degree of development of the embryos. They are names which make it possible to identify the embryos in the collections.

Age in days	Total length and head-length (hl) in mm	Section direction	Thickness (microns)	Staining	Reconstructions	Magnification	Sources
				Lepidochelys olivacea			
8	9	transv.	6	—	*graph.c.l.* and *i.*	41	S
8	8	horiz.	8	—	—	—	S
—	9,3	transv.	10	—	—	—	S
—	10	transv.	10	—	—	—	L
—	10,3	transv.	10	—	—	—	L
—	10,5	transv.	10	—	—	—	L
—	11	transv.	10	—	—	—	L
10	10	transv.	8	—	*graph.c.l.* and *i.*	31	S
9	11	transv.	8	—	*graph.c.l.* and *i.*	31	S
10	—	transv.	8	—	*wax-pl.ventr.gr.*	63	S
11	10	transv.	8	—	*graph.c.l.* and *i.*	31	S
12	10,5	transv.	8	—	*graph.c.l.**, *i.* and *nuclei**	31	S
—	—	—	—	—	*wax-pl.ventr.gr.*	63	
14	—	transv.	8	—	*graph.c.l.**, *i.* and *nuclei**	31	S
—	—	—	—	—	*wax-pl.ventr.gr.*	63	—
15	—	transv.	8	—	*gr.graph.c.l.* and *i.*	31	S
16	14 (6,5 hl)	transv.	8	—	*dr.graph.c.l.* and *i.*	31	S
17	13 (5 hl)	transv.	8	—	*dr.graph.c.l.* and *i.*	31	S
18	—	transv.	8	—	—		S
19	—	transv.	8	—	—		S
20	—	transv.	8	—	—		S
21	16	transv.	8	—	—		S
22	18 (8 hl)	transv.	10	—	*dr.graph.c.l.*, *i.* and *nuclei*	25	S
23	—	transv.	10	—	—	—	S
24	—	transv.	10	—	—	—	S
26	29 (9 hl)	transv.	10	—	*dr.graph.c.l.*, *i.* and *nuclei*	10	S
28	31 (10 hl)	transv.	10	—	*graph.c.l.*, *i.** and *nuclei*	25	S
				Chrysemys marginata			
—	1,64 hl	transv.	10	—	*graph.c.l.* and *i.*	50	S
—	2,03 hl	transv.	10	—	—	—	S
—	2,72 hl	transv.	10	—	*graph.i.*	50	S
—	2,19 hl	transv.	10	—	*graph.c.l.*, *i.* and *nuclei*	50	S

VOL. 34 1953

Age in days	Total length and head-length (hl) in mm	Section direction	Thickness (microns)	Staining	Reconstructions	Magnification	Sources
—	2,38 hl	transv.	10	—	—	—	S
—	2,53 hl	transv.	10	—	—	—	S
—	2,65 hl	sag.	10	—	—	—	S
—	3,4 hl	transv.	10	—	—	—	S
—	3,59 hl	transv.	10	—	—	—	S
—	3,6 hl	transv.	10	—	—	—	S
—	3,67 hl	transv.	10	—	—	—	S
—	3,99 hl	transv.	10	—	—	—	S
—	4,29 hl	transv.	10	—	—	—	S
—	4,4 hl	transv.	10	—	*graph.i.* and *nuclei*	25	S
—	4,68 hl	transv.	10	—	—	—	S
—	5 hl	transv.	10	—	—	—	S
—	6,5 hl	transv.	10	—	—	—	S
—	Carapax length						
	7	transv.	10	—	—	—	S
—	8,24	transv.	10 and 15	—	—	—	S
—	11	transv.	10	—	*graph.i.* and *nuclei*	25	S
—	12	transv.	10	—	—	—	S
—	22	transv.	15	—	—	—	S
juv.	—	transv.	10	—	*graph.i.* and *nuclei*	25	S
—	4	transv.	10	—	*wax-pl.e.l.* and *i.*	200	L
—	4,5	transv.	10	—	*wax-pl.e.l.* and *i.*	200	L
—	6,5	transv.	10	—	*wax-pl.e.l.* and *i.*	200	L
—	—	—	—	—	*graph.i.*	50	L
			Dermochelys coriacea				
10	—	transv.	6	—	—	—	S
11	6,5	transv.	10	—	—	—	L
12	—	transv.	8	—	—	—	S
15	8	transv.	10	—	—	—	S
15	—	transv.	8	—	—	—	S
17	—	transv.	8	—	—	—	S
19	—	transv.	8	—	—	—	S
21	—	transv.	8	—	—	—	S
29	—	transv.	10	—	—	—	S
			Trionyx japonica				
37	—	transv.	10	—	—	—	S

Age in days	Total length and head-length hl) in mm	Section direction	Thickness (microns)	Staining	Reconstructions	Magnification	Sources
				Tropidonotus natrix			
—	3,61 hl	transv.	10	—	—	—	S
—	3,91 hl	transv.	10	—	—	—	S
—	4,00 hl	transv.	10	—	—	—	S
—	4,18 hl	transv.	10	—	—	—	S
—	4,34 hl	transv.	10	—	—	—	S
—	4,42 hl	transv.	10	—	—	—	S
—	5,1 hl	transv.	10	—	—	—	S
—	5,3 hl	transv.	15	—	—	—	S
—	5,53 hl	transv.	10	—	—	—	S
—	5,88 hl	transv.	10	—	—	—	S
—	6,06 hl	transv.	10	—	—	—	S
—	6,88 hl	transv.	15	—	—	—	S
—	7 hl	transv.	15	—	—	—	S
—	7,5 hl	transv.	15	—	—	—	S
—	8 hl	transv.	15	—	—	—	S
—	14	transv.	15	—	*wax-pl.c.l.* and *i.*	100	L
—	—	—	—	—	*graph.i.*	100	—
—	105 hl	transv.	15	—	—	—	S
—	110 hl	transv.	15	—	—	—	S
—	130 hl	transv.	10	—	—	—	S
ad.	—	horiz.	40	Mallory's phosphotungstic acid haematoxylin	—	—	ZL
ad. nr. 515	—	sag.	60	Mallory's phosphotungstic acid haematoxylin	—	—	ZL
fullturm embryo	165	horiz.	12	Haematoxylin-acid fuchsin—Light green	—	—	ZL
				Vipera berus			
—	48 nr. 344	sag.	8	—	—	—	ZL
—	48 nr. 345	transv.	8	—	—	—	ZL
—	80 nr. 342	transv.	8	—	—	—	ZL
new born offspring		transv.	10	—	—	—	ZL

Age in days	Total length and head-length hl) in mm	Section direction	Thickness (microns)	Staining	Reconstructions	Magnification	Sources
nr. 339 e ad. nr. 182		sag.	10	—	—	—	ZL
			Lacerta agilis				
ad.	nr. 562	transv.	6	Gomori-haematoxylin-phloxine	—	—	ZL
			Sceloporus orcutti				
ad.	nr. 474	transv.	40	Mallory's phosphotungstic acid haematoxylin	—	—	ZL
			Chalcides tridactylus				
—	9,5 (1 hl)	transv.	10	—	—	—	S
juv.	—	transv.	10	—	—	—	S
			Alligator sp.				
—	17 hl	transv.	15	—	—	—	S
—	15	transv.	15	—	*wax-pl.c.l.* and *i.*	33	L
—	—	—	—	—	*graph.i.*	50	—
—	24	transv.	15	—	*graph.i.*	33	L
—	34	transv.	15	—	*graph.i.*	33	L
			Crocodilus niloticus				
juv.	—	transv.	20	—	—	—	S
			Columba livia				
—	23	transv.	15	—	—	—	L
—	33	transv.	15	—	—	—	L
ad.	nr. 557	horiz.	6	Gomori-haematoxylin	—	—	ZL

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VOL. 34 1953

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VOL
34
195

VOL.
34
1953

ERRATA STATEMENT.

In M. K. M. Rao and L. S. Ramaswami: "The fully formed Chondrocranium of Mabuya with an account of the adult Osteocranium", published in Acta Zoologica, 1952, part 3, the following errata should be corrected:

page 218, *delete* lines 25—38,

„ 228, line 4 from the bottom: *read* The bulbus oculus *instead of* the bulbus oculi,

„ 235, line 2 in text: *read* spheno-ethmoidalis *instead of* spheno ethmoidalis,

„ 236, lines 6 and 7: *read* broadened *instead of* broadended,

„ 251, legend of fig. 17, line 4: *read* right (a″a″) *instead of* right (a′a′),

„ 264, line 9: the italicised head-line should be in roman,

„ 270, lines 10 and 11 from the bottom: *read* We are *instead of* I am.

VOL
34
195

L'OOGENESI NEGLI ORTOTTERI. I. RICERCHE ISTOLOGICHE E CITOMETRICHE IN *ANACRIDIUM AEGYPTIUM* L. DALLA SCHIUSA ALL'IMAGINE

PER

GIUSEPPE COLOMBO

(Istituto di Zoologia e Anatomia comparata dell'Università di Padova, diretto dal Prof. Umberto D'Ancona.)

VOL. 34 1953

CONTENUTO.

Introduzione 191
Materiale e metodo 193
I. Modificazioni dell'ovario nel corso dello sviluppo larvale e nei primi periodi dello stadio imaginale 194
II. Considerazioni sul ciclo oogenetico 200
III. Le trasformazioni degli oogoni in oociti 201
IV. La struttura nucleare e cromosomica nella profase meiotica 204
V. L'apparato siderofilo (endonucleare) 212
VI. L'accrescimento oocitario 217
Riassunto e Conclusioni 227
Conclusions and summary 228

INTRODUZIONE.

L'ovario degli Ortotteri è di tipo panoistico, gli oociti sono di tipo alimentare follicolare (secondo KORSCHELT 1886).

La segregazione delle cellule germinali avviene dall'entoderma, prima che si inizi la segregazione dello strato mesodermico interno. L'abbozzo della gonade raggiunge la posizione definitiva, dorsale, alla blastocinesi; dopo tale stadio si ha la differenziazione sessuale della ghiandola (NELSEN 1933). Prima della schiusa, gli ovarioli sono già formati. Alla schiusa e fin dopo la seconda muta nell'ovario si trovano oogoni, preoociti, oociti nel primo periodo di accrescimento e meno numerosi nel secondo periodo di accrescimento, negli stadi successivi aumentano gli oociti nel secondo periodo di accrescimento. Nell'imagine, subito dopo l'ultima muta, l'ovario consta di pochi preoociti ed oociti in primo periodo di accrescimento e, nella gran parte, di oociti in grande accrescimento. La maturazione dell'uovo avviene di solito alcune settimane ed a volte alcuni mesi dopo l'ultima muta. (NELSEN 1933, MCNABB 1928, PHIPPS 1950).

I primi stadi di formazione dell'ovario sono stati studiati da HEYMONS (1895) in *Phillodromia (Blatta) germanica, Gryllus domesticus, Gryllus campestris, Periplaneta orientalis,* da WHEELER (1893) in *Xiphidium ensiferum* e più recentemente da NELSEN (1933) in *Melanoplus differentialis.*

L'intero processo oogenetico è stato studiato da PEHANI (1925) in *Carausius morosus;* da MATTHEY (1941—1945) in *Saga pedo* Pallas ed in *Pycnoscelus surinamensis;* le ultime fasi (maturazione e fecondazione) da BLOCHMAN (1887) e da WHEELER (1889) in *Blatta germanica,* da VON BAEHR (1907) in *Bacillus rossii,* da MCNABB (1928) in *Chortophaga viridifasciata* ed in *Circotettix verruculatus.*

Le più antiche di queste ricerche furono eseguite allo scopo di indagare problemi citologici della maturazione, ormai risolti (BLOCHMAN, WHEELER, VON BAEHR); altre sono in relazione ai problemi citologi e citogenetici della partenogenesi (PEHANI, MATTHEY) o al comportamento cromosomico nella oogesi in confronto con la spermatogenesi. (MCNABB.)

I problemi citologici legati all'accrescimento oocitario negli Ortotteri sono stati solo parzialmente indagati: GIARDINA (1902) si è occupato del secondo periodo di accrescimento degli oociti di *Mantis religiosa;* MURRAY (1926) ha studiato la funzione secretrice delle cellule follicolari nei grilli; NATH e MOHAN (1929) hanno indagato il comportamento di alcuni componenti citoplasmatici (condrioma, apparato del Golgi ecc.) nell'oogenesi di *Periplaneta americana;* PAINE (1932) ha studiato i corpi del Golgi negli oociti di *Oecanthus quadripunctatus* Bent; BUCHNER (1909) ha studiato l'oogenesi di *Grillus campestris* occupandosi in modo particolare del comportamento dell'eterocromosoma e dell'apparato nucleolare; JÖRGENSEN (1913) nel suo studio comparativo dell'apparato nucleare riporta dei dati riguardanti gli oociti in accrescimento di *Blatta, Decticus, Gryllotalpa;* VOINOV (1924) ha descrito alcuni stadi dell'oogenesi di *Gryllotalpa vulgaris* descrivendo in particolare il comportamento cromosomico nelle prime fasi meiotiche. Più recentemente BAUER (1931) ha studiato assieme agli oociti di altre specie di Insetti, anche quelli di *Stenobothrus,* indagando col metodo di Feulgen le modificazioni dei cromosomi nel 2° periodo di accrescimento (cioè la scomparsa dell'acido desossiribonucleico).

In lavori di citologia piuttosto vecchi (verso la fine del secolo scorso) si trovano dati che si riferiscono anche agli oociti degli Ortotteroidi, e così pure in lavori recenti si trovano osservazioni citologiche sullo stesso materiale, ma che interessano solo indirettamente il processo oogenetico. Queste ricerche verranno prese in considerazione nelle note successive in relazione ai problemi particolari che verranno studiati.

In complesso le ricerche citologiche sulla oogenesi degli Ortotteri sono molto meno numerose di quelle sull'oogenesi di altri ordini di Insetti e di gran lunga più limitate di quelle sulla spermatogenesi degli Ortotteri stessi, che si può dire formino la base delle nostre conoscenze sulla meiosi degli animali. La

causa di ciò va probabilmente attribuita al fatto che una ricerca completa sui primi processi oogenetici deve essere eseguita su larve dei primi stadi di sviluppo usando perciò esclusivamente specie che si possono riprodurre ed allevare in laboratorio.

Dal punto di vista citologico gli oociti degli Ortotteri ad un esame sommario sembra non presentino strutture caratteristiche come si trovano in quelli degli altri ordini di Insetti ad ovari non panoistici. Però quando si può avere il materiale completo, gli oociti degli Ortotteri si prestano molto bene per lo studio di molti problemi citologici fondamentali, quali l'accrescimento oocitario, le trasformazioni cromosomiche che l'accompagnano (prime fasi meiotiche, formazione dei «lamp-brush chromosomes») ed il comportamento degli apparati nucleolo-simili, sopratutto se visti alla luce delle attuali conoscenze sulla morfologia e fisiologia cellulare e nucleare.

OL.
34
953

Io ho iniziato lo studio dell'oogenesi di *Anacridium aegyptium* L. per esaminare alcuni problemi citologici particolari e altri riguardanti il ciclo biologico di questa specie che sto allevando in laboratorio e di cui ho già studiato alcune questioni citologiche della spermatogenesi. (COLOMBO 1951.)

In queste prime osservazioni, presentate in via preliminare in una comunicazione al Convegno dell'Unione Zoologica Italiana del 1952 a Milano, riferisco semplicemente i dati di esami istologici fatti con le tecniche usuali ed i risultati di osservazioni citometriche sull'ovario dalla schiusa allo stadio imaginale. Spero seguiranno quanto prima ulteriori osservazioni su altri stadi di sviluppo dell'ovario e quelle riguardanti il comportamento istochimico degli oociti.

MATERIALE E METODO.

Sono state adoperate larve, appena schiuse e nei successivi stadi di sviluppo fino all'imagine, di *Anacridium aegyptium* L. allevate in camera termoregolata a 28° ± 1° C. ed alimentate con foglie di ligustro, (per la tecnica di allevamento, v. COLOMBO 1951).

Le osservazioni sono state fatte su ovari fissati e sezionati e su preparati per schiacciamento. Nei primi stadi larvali, per la difficoltà di isolare e maneggiare i piccoli ovari ho fissato o tutto l'animale oppure i segmenti addominali; dopo la 4ª e la 5ª muta è abbastanza facile invece isolare e fissare le singole ghiandole genitali. Ho adoperato vari fissativi: per larve intere Dubosq-Brazil o Carnoy; per i segmenti addominali e per gli ovari isolati Carnoy, Zenker formolico, Sanfelice. La disidratazione e lo schiarimento sono stati fatti coll'alcool butilico e l'inclusione in paraffina, secondo i tempi riportati in «McClung's Handbook of Microscopical Technique».

Le sezioni di vario spessore, a seconda della necessità, sono state colorate con l'ematossilina ferrica di Heidenhain (metodo rapido secondo Cleveland),

con l'emallume-saffranina-orange, colla reazione di Feulgen, col metodo di Unna-Pappenheim a vari pH secondo Gerola e Vannini e col cresilvioletto. Sono stati anche esaminati ovari di imagini raccolte in natura in autunno, cioè parecchi mesi prima della deposizione, che avviene a Padova in marzo-aprile-maggio secondo l'andamento stagionale.

Per lo studio dei nuclei nei primi stadi dell'oogenesi sono risultati molto utili i preparati per schiacciamento eseguiti secondo la tecnica usuale, cioè: fissazione in acido acetico al 45 % per 10—20 minuti, schiacciamento su vetrino albuminato, permanenza per 12 ore dei vetrini in alcool a 95° acidificato con alcune gocce di acido acetico, distacco dei vetrini e colorazione col metodo di Feulgen o con l'ematossilina ferrica.

Sono state fatte anche osservazioni a fresco, preliminari per le ricerche ulteriori. I primi stadi oocitari sono difficili da trovare a fresco perchè le cellule germinali si trovano in mezzo a numerosi altri elementi; facilmente si possono osservare invece gli oociti in accrescimento. I preparati sono stati fatti dissezionando un pezzo di ovario in soluzione di Ringer-Lock-Banta (Kanô 1951); isolati alcuni ovarioli, questi venivano posti su un copriogetto con una piccola goccia di soluzione e tutto veniva ricoperto con olio di vaselina, il vetrino veniva quindi capovolto su un portaoggetto incavato; in tal modo gli oociti sopravvivevano per alcune ore senza presentare alterazioni e mantenendo la loro forma regolare.

Le misure delle cellule germinali nei primi stadi sono state fatte sui preparati per sezione da disegni fatti con la camera chiara (Leitz), negli stadi più avanzati (oociti in accrescimento) sui preparati a fresco direttamente con un oculare micrometrico.

I. MODIFICAZIONI DELL'OVARIO NEL CORSO DELLO SVILUPPO LARVALE E NEI PRIMI PERIODI DELLO STADIO IMAGINALE.

Alla schiusa l'ovario si presenta già distinto in ovarioli rudimentali e rimane pressochè della medesima struttura sino alla 2ª muta.

In sezione frontale esso appare formato come da tante vescicole di forma ovoidale che si staccano da un doppio rafe mediano al quale sembrano attaccate come ad un peduncolo. (Fig. 1.)

Questo apparente rafe madiano è formato da cellule mesodermiche (da molti AA. dette epiteliali), allineate ed addensate, con poco citoplasma e nuclei molto colorabili con l'ematossilina e con la Feulgen, di forma ovoidale; esso effettivamente consiste dei filamenti terminali e della parte apicale dell'abbozzo del germario, disposti in senso cefalo-caudale.

Dai filamenti terminali con un angolo di 90°, cioè in direzione laterale, si continuano gli abbozzi del germario e del vitellario.

VOL. 34 1953

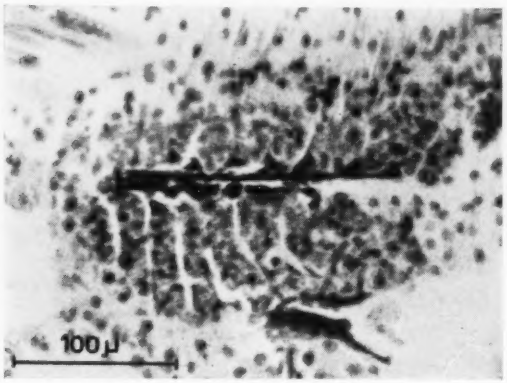

Fig. 1. Ovario di larva al 2° stadio, sezione frontale. Fiss. Sanfelice; color. Feulgen.

La parte più apicale della porzione degli ovarioli, posta in senso laterale, è molto sottile ed è formata da singole cellule con nucleo grosso, basofilo, a filamenti cromatici spessi, con scarso citoplasma intorno, circondate da cellule più piccole a nuclei ovali o reniformi con citoplasma molto scarso. I primi sono oogoni primari circondati da potenziali cellule follicolari.

Procedendo verso la base dopo una distanza corrispondente a due o al mas-

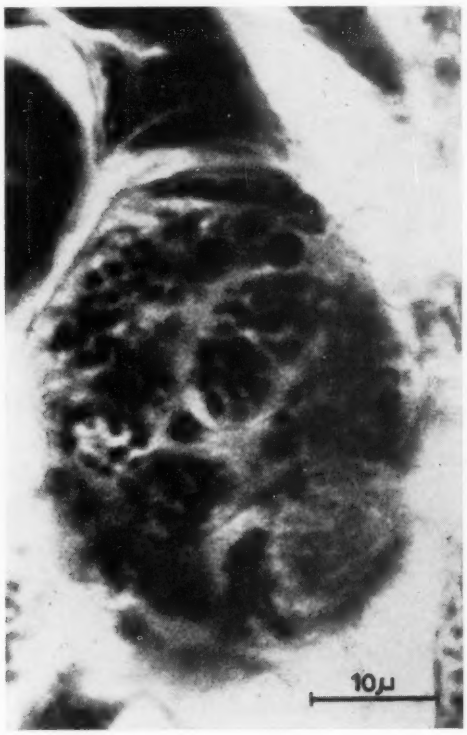

Fig. 2. Sezione longitudinale obliqua di apice di ovariolo di larva al 1° stadio. Fiss. Sanfelice; color. emal.-safranina-orange.

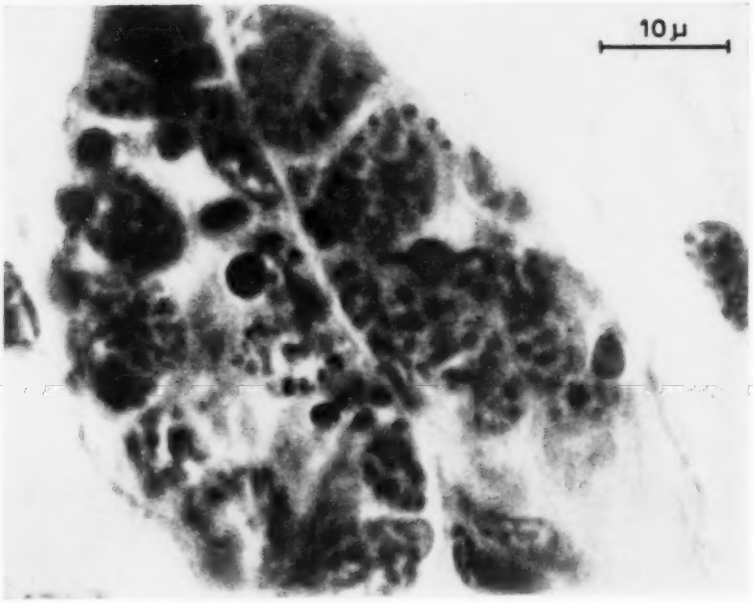

Fig. 3. Sezione longitudinale della parte apicale di due ovarioli di larva al 1° stadio. Fiss. Sanfelice; color. emal.-safranina-orange.

simo tre oogoni primari circondati dalle proprie cellule follicolari, gli ovarioli si ingrossano bruscamente (fig. 2 e 3). Vi si possono distinguere una parte apicale ed una basale. La parte apicale è formata da nidi di 5—6 cellule a nucleo sferico od ovoidale, piuttosto grosso, con relativamente scarso citoplasma, dell'aspetto complessivo di oogoni secondari, circondati dalle cellule follicolari potenziali a nuclei reniformi (fig. 4). La sezione trasversale di un ovariolo comprende di solito più di un nido; in questi nidi sono frequenti le mitosi.

I nidi situati più lontano dall'apice dell'ovariolo presentano una delle cellule germinali (oogonio terziario) distinguibile dalle altre per il citoplasma più

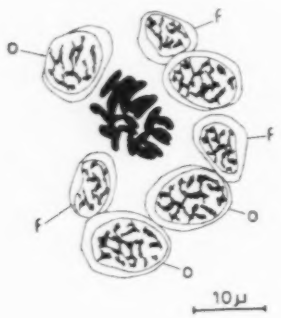

Fig. 4. Ooogoni II (o) di cui uno in mitosi tra potenziali cellule follicolari (f). Color. Feulgen.

VOL. 34 1953

abbondante ed il nucleo ingrossato; nel nucleo i corpi cromatici appaiono più distinti ed anche il carioplasma è Feulgen-positivo. Questo oogonio o preoocita è circondato da altri elementi sempre a scarso citoplasma ed i cui nuclei, a carioplasma non colorabile, presentano i filamenti cromosomici allungati ed orientati in modo da sembrare delle pseudo-ana-telofasi o pseudo-profasi; molto spesso vi sono anche nuclei molto più piccoli, nuclei picnotici e forse talora cromosomi isolati.

In mezzo a queste cellule ed attorno all'oogonio centrale si trovano constantemente zolle o gocciole intensamente basofile, che si colorano oltre che con l'ematossilina, con la saffranina, la pironina ed alcune, le più grosse, con il metodo di Feulgen.

Tutto il quadro morfologico delle trasformazioni che si osservano dai nidi a più oogoni a quelli con un singolo oogonio fa pensare che si tratti di una degenerazione della maggior parte degli oogoni con eliminazione di sostanza basofila e trasformazione di una o due cellule germinali in preoociti e quindi in oociti premeiotici.

Tutti i nidi di oogoni, anche quelli in cui ne rimane uno centrale che si trasforma in preoocita, sono circondati, non però completamente, dalle cellule follicolari potenziali, di forma un po' irregolare, a nucleo reniforme o triangolare, ma tuttavia abbastanza grande, basofilo e Feulgen-positivo con carioplasma intensamente colorabile ed a filamenti cromosomici grossi e ben visibili, cellule sempre abbastanza bene distinguibili dagli elementi germinali.

Nella parte più basale dell'ovariolo ingrossato, immediatamente seguente alle regioni sopra descritte, si trovano oociti nelle prime fasi meiotiche ed in primo periodo di accrescimento; questa parte corrisponde all'abbozzo del cosidetto vitellario. Gli ovociti derivano direttamente da singoli oogoni che rimangono isolati nei nidi. Le modificazioni premeiotiche e meiotiche del nucleo, come pure l'accrescimento nucleare e citoplasmatico saranno descritti dettagliatamente più sotto.

Anche gli oociti sono circondati, non completamente, dalle cellule follicolari potenziali che son principalmente localizzate ai poli apicale e basale degli oociti stessi.

Il filamento apicale e le parti ingrossate degli ovarioli sono ravvolte da una membrana sottile, formata da cellule appiattite, piuttosto grandi con nuclei distanziati l'uno dall'altro, intensamente basofili, a struttura compatta, in ogni caso ben distinguibili anche dalle potenziali cellule follicolari.

All'estremità basale gli ovarioli si attaccano all'abbozzo dell'ovidotto che è un tubo cilindrico formato da cellule di tipo epiteliale, monostratificate, a lume molto piccolo, nei primissimi stadi e nella parte caudale virtuale.

Dopo la seconda muta gli ovari cominciano ad assumere un aspetto diverso da quello sopradescritto e vengono ad assomigliare nettamente agli ovari non maturi delle imagini. (Fig. 5.)

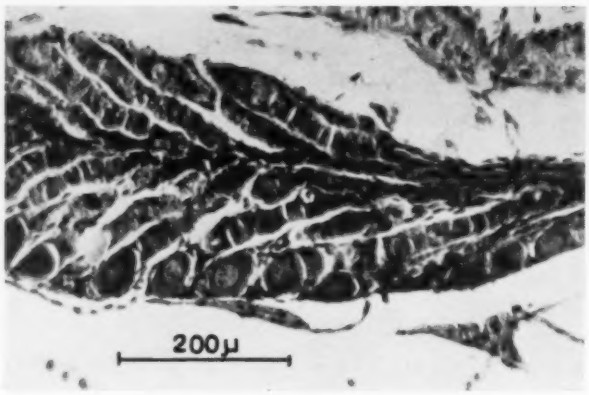

Fig. 5. Ovario di larva al 4° stadio, sezione frontale. Fiss. Carnoy; color. emat. ferr. Heidenhain.

VOL. 34 1953

Scompare il cordone mediano o meglio si viene a capire nettamente come esso sia formato dai filamenti terminali riuniti dorsalmente.

Poichè la parte basale degli ovarioli si sposta caudalmente e la parte apicale rimane pressochè nella stessa posizione, gli ovarioli vengono a disporsi obliquamente in direzione medio laterale e cefalo-caudale, cioè il germario ed il vitellario si allineano con l'asse del filamento terminale pur restando la parte basale posta lateralmente (negli stadi precendenti la parte ingrossata degli ovarioli faceva un angolo di 90° con il filamento terminale stesso).

La struttura dell'intero ovariolo apparentemente risulta molto modificata rispetto a quella descritta per i primi stadi larvali.

Il filamento terminale è sempre costituito da un cordone di cellule stipate tra loro con poco citoplasma e nuclei piuttosto piccoli ovalari, talora reniformi. E' forse possibile talvolta distinguere in mezzo a queste cellule degli elementi a nuclei più grossi rotondi, che si riconoscono come oogoni primari. Tutti i nuclei sono fortemente basofili e Feulgen-positivi a struttura relativamente compatta.

Distalmente al filamento terminale, specialmente prima della quarta muta, si trovano alcuni nidi di oogoni avvolti dalle potenziali cellule follicolari; distalmente a questi, nidi con oogonio centrale in procinto di trasformarsi in oocita con attorno elementi cellulari in degenerazione e zolle o gocciole di sostanza basofila. Complessivamente il quadro è identico a quello descritto per gli stadi precedenti colla differenza che, in questi stadi, gli ovarioli in questa regione sono più sottili ed un singolo nido di oogoni riempie tutta la sezione dell'ovariolo.

Questa porzione degli ovarioli si può forse chiamare germario.

Distalmente alla regione degli oogoni si trova quella degli oociti che occupano la maggior lunghezza degli ovarioli. Nella parte prossimale il filamento ovarico è piuttosto sottile, la sezione è occupata da una e talora da due oociti nel primo

periodo di accrescimento, non ancora molto voluminosi, circondati o meglio separati prossimalmente e distalmente da un gruppo di potenziali cellule follicolari che si presentano a nucleo allungato con l'asse maggiore disposto in direzione trasversale.

Nella parte più distale degli ovarioli si trovano gli oociti in secondo periodo di accrescimento, molto più grandi, completamente avvolti dalle cellule follicolari. Queste per moltiplicazione cariocinetica negli ultimi stadi larvali vengono a costituire attorno a ciascun ovocita uno strato continuo a cellule basse, piuttosto piatte, con nucleo relativamente grosso a cromosomi compatti, tipico delle cellule in attiva moltiplicazione. In questo strato le mitosi sono frequenti.

Anche dopo l'ultima muta non si riesce a vedere, all'esame microscopico, alcuna attività secretoria delle cellule follicolari. Solo negli ovari imaginali dopo qualche settimana dall'ultima muta attorno agli oociti più grossi ciascuna cellula follicolare risulta separata dall'oocita stesso da una semiluna anista che forse sta ad indicare l'inizio di una attività secretoria delle cellule stesse. Tra oocita ed oocita vi sono sempre gruppi di cellule simili a quelle follicolari. All'estremità basale dell'ovariolo vi è un ammasso di cellule morfologicamente simili alle follicolari, che uniscono ciascun ovariolo con l'abbozzo dell'ovidotto.

L'ovidotto, man mano che l'ovario si sviluppa, si dilata per moltiplicazione delle cellule che ne costituiscono la parete. Il lume nei primi stadi, appare al microscopio completamente vuoto; negli stadi imaginali piuttosto avanzati vi si può vedere della sostanza acidofila di struttura omogenea.

Ciascun ovariolo, dal filamento apicale alla base, e così pure l'ovidotto sono avvolti da una membrana di cellule laminari molto grandi con nucleo piccolo, a struttura compatta. Specialmente nei primi stadi questa lamina cellulare pare continuarsi col tessuto adiposo circostante.

Oociti in accrescimento si trovano quindi fin dai primi stadi larvali, aumentano in numero e in volume col procedere dello sviluppo.

La vitellogenesi vera e propria, cioè la formazione di tuorlo globulare nel citoplasma degli ovociti, si comincia ad osservare negli ovari di ♀♀ parecchio tempo dopo che hanno raggiunto lo stadio imaginale.

Se si esaminano a fresco gli ovari di ♀♀ poche settimane dopo l'ultima muta o di quelle raccolte in natura in autunno, essi risultano formati da numerosi ovarioli piuttosto lunghi, costituiti da una serie di follicoli ovarici formati da oociti in accrescimento avvolti dalle cellule follicolari. Gli ovociti posti più vicini all'ovidotto sono i più grandi; procedendo verso la parte apicale dell'ovariolo si trovano quelli gradualmente più piccoli. Nella parte terminale si trova il germario costituito da ovociti nelle prime fasi meiotiche in mezzo alle potenziali cellule follicolari; questa porzione dell'ovariolo non si può esaminare a fresco perchè non si possono isolare le singole cellule.

La serie di ovociti ben visibili comprende, cominciando dal germario, oociti in fase iniziale o media del 2° periodo di accrescimento: sono cellule di forma

sferica irregolare di circa 500 μ di diametro con un nucleo di circa 300 μ. Questi oociti non sono completamente avvolti dalle cellule follicolari; man mano che si procede verso la base dell'ovariolo si trovano oociti sempre più grandi, prima a diametri uguali tra loro, quindi con il diametro parallelo all'asse dell'ovariolo molto allungato, così che assumono una forma elissoidale; il nucleo è sempre sferico. Il citoplasma degli oociti più piccoli risulta, a fresco, completamente omogeneo; globuli di tuorlo si cominciano a vedere negli oociti un po' allungati, con l'asse trasverso di circa 1 500 μ e quello longitudinale di circa 2 500 μ.

Non sono ancora riuscito a procurarmi una serie sufficente di ovari per poter ricostruire tutte le successive modificazioni degli oociti durante la vitellogenesi fino alla deposizione.

II. CONSIDERAZIONI SUL CICLO OOGENETICO.

Dall'esame istologico dell'ovario nei vari stadi di sviluppo possiamo farci una idea complessiva del ciclo oogenetico dell'*Anacridium*.

Già prima della schiusa l'ovario presenta la struttura ad ovarioli ed in questi si trovano già oociti in profase meiotica. Fino alla 2ª—3ª muta gli ovarioli contengono oogoni ed oociti nel primo periodo di accrescimento; dopo la terza muta si trovano principalmente oociti nel primo e nel secondo periodo di accrescimento. Negli ultimi stadi larvali e dopo l'ultima muta ciascun ovariolo è composto per la maggior parte del suo volume da oociti in secondo periodo di accrescimento più o meno avanzato, nella parte apicale si trovano ancora oociti in leptotene ed in zigotene.

La vitellogenesi vera e propria comincia quando gli oociti hanno raggiunto un dato grado di accrescimento e le cellule follicolari hanno completamente avvolto l'oocita con uno strato epitelio-simile.

La vitellogenesi negli Ortotteri avviene principalmente, per quanto si conosce, per azione delle cellule follicolari (Murray 1926), le quali secernono successivamente il corion. Questi ultimi processi sono regolati anche per gli Ortotteri come per gli altri Insetti dai «corpora allata», come ha visto e dimostrato in *Melanoplus differentialis* Weed Pfeiffer (1945).

E' interessante notare che negli Insetti il processo oogenetico procede complessivamente attraverso diverse tappe analoghe a quelle che si trovano per es. nei Vertebrati; anche negli Insetti, come nei Vertebrati, vitellogenesi e deposizione sono regolate da ormoni (dai «corpora allata» e dall'ipofisi rispettivamente); mentre le altre fasi dell'oogenesi non sembrano regolate da alcuna correlazione umorale specifica.

In generale il ciclo vitale degli Acrididi dura un anno e dopo un numero vario di deposizioni le ♀♀ muoiono.

In *Locusta migratoria migratorioides* R. e F. Norris (1950) hanno osser-

VOL. 34 1953

vato, in laboratorio, fino ad oltre 8 deposizioni per femmina; sulla stessa specie PHIPPS (1950) ha trovato che ad ogni deposizione altri oociti entrano in vitellogenesi e vi sono sempre, in ciascun ovariolo, follicoli ovarici a vari stadi di maturazione.

Le femmine di *Anacridium aegyptium* allevate in laboratorio presentano un numero vario di deposizioni: in base ad osservazioni non ancora pubblicate, perchè si riferiscono ad un numero non ancora sufficientemente vasto di esemplari (circa 10), ho potuto osservare fino a 9 deposizioni (con in media circa 40 uova per deposizione) per ♀.

Gli ovari di ♀♀ sacrificate o morte dopo l'ottava o nona deposizione contenevano ancora ovociti in vitellogenesi avanzata ed in varie fasi di accrescimento; il germario era ridotto e conteneva un numero ridotto di oociti in profase meiotica iniziale. In ovari di ♀♀ di *Anacridium* poco tempo dopo l'ultima muta ho contato circa 15—18 oociti in secondo periodo di accrescimento ed in vitellogenesi iniziale, per ovariolo; in ♀♀ dopo 9 deposizioni pure circa 15—20 ovociti per ovariolo a varî stadi di accrescimento. Perciò si può ammettere con buona probabilità che l'accrescimento oocitario (2° periodo) continui durante tutta la vita imaginale, e che negli ovociti, che hanno raggiunto un determinato stadio, cominci la vitellogenesi appena entrano in funzione i «corpora allata». Il numero di uova deposte per ciascun ovariolo non giunge mai ad esaurire il numero di ovociti pronti per la vitellogenesi e per la deposizione: la morte dell'animale oppure la diminuzione senile del metabolismo bloccano le fasi terminali dell'ovogenesi.

Non sembra che per gli Acrididi vi siano cicli riproduttivi pluriannuali; questi eventualmente potrebbero essere regolati da fattori ormonali che agirerebbero sulle ultime fasi dell'oogenesi, come avviene per esempio nei Ditiscidi (JOLY, 1945). Praticamente la maturazione e la deposizione continuano, non fino all'esaurimento dell'ovario, ma fino alla senilità o la morte dell'animale.

Queste considerazioni hanno importanza nella valutazione della capacità riproduttiva: la differenza di fecondità entro una stessa specie non può essere valutata dal numero di ovarioli o di oociti che si trovano in ciascun ovario; praticamente hanno importanza i fattori ambientali che influiscono sul metabolismo generale e contemporaneamente nelle prime fasi dell'oogenesi, e quelli che agiscono sull'attività dei «corpora allata» e perciò nelle fasi finali dell'oogenesi stessa.

III. LE TRASFORMAZIONI DEGLI OOGONI IN OOCITI.

Gli oogoni primari si trovano difficilmente negli ovari delle larve anche più giovani; se ne vedono nella parte apicale sottile dell'abbozzo del germario subito dopo la schiusa, come è stato descritto sopra. Essi sono completamente e stret-

tamente circondati dalle potenziali cellule follicolari, si differenziano da queste solo per avere un nucleo rotondeggiante ed un po' più di citoplasma. Un accurato esame citologico è praticamente impossibile.

Gli oogoni secondari si trovano in nidi di 5—6 elementi; sono cellule a scarso citoplasma, a nucleo rotondeggiante. Frequenti nei nidi sono le mitosi che si possono osservare in tutti gli stadi; i nuclei interfasici, nei preparati per schiacciamento, appaiono a cromatina filamentosa, relativamente contratta. (Fig. 4.)

Come ho descritto più sopra, nei nidi di oogoni meno apicali si trovano zolle extracellulari di sostanza che dal punto di vista tintoriale si può considerare cromatinica (A.R.N.) (fig. 2 e 3). Al centro dei nidi in cui sono più evidenti queste formazioni, in generale si distingue un oogonio più grande, circondato da altri elementi cellulari, che a parer mio sono pure oogoni in degenerazione (in picnosi o in carioressi).

E' molto probabile che vi sia una relazione diretta fra questa eliminazione di sostanza nucleare e la trasformazione dell'oogonio centrale, che ormai si può considerare preoocita. Si tratterebbe di una specie di secrezione di sostanza nucleare (A.R.N.) eliminata da cellule germinali che vanno in degenerazione ed utilizzata da un oogonio, che diventa, forse per azione di questa sostanza stessa, un oocita.

Voinov (1924) in un lavoro sull'oogenesi di *Gryllotalpa vulgaris,* riporta le stesse osservazioni e le interpreta direttamente come una degenerazione di tutti gli oogoni di ciascun nido, salvo uno che si trasforma in oocita.

La questione è molto più complicata di quanto possa sembrare; queste osservazioni possono essere un contributo all'ipotesi di Montalenti (1948), che la meiosi sia regolata dalla presenza di A.R.N. extracellulare. Purtroppo la documentazione sperimentale è piuttosto scarsa (Huskins e Kodani 1949). Fenomeni analoghi sono stati osservati anche nella spermatogenesi delle cavallette (Battaglia B. 1950) in cui nei follicoli testicolari tra gli spermatogoni si trovano appunto zolle e granuli di A.R.N. In osservazioni personali, non pubblicate, ho potuto osservare anch'io che sostanza cromatinica si trova sino a livello degli spermatociti, cioè sarebbe in relazione con l'entrata in meiosi degli spermatogoni, però non è possibile definire se vi sia degenerazione di elementi germinali. E' probabile che molte degenerazioni di cellule germinali a livello degli spermatogoni (cfr. Sarà 1950) non siano che aspetti diversi dello stesso processo.

L'oogonio che è così diventato un preoocita presenta un aumento del volume del nucleo e del citoplasma. Il nucleo perde la leggera, ma netta basofilia e Feulgen-positività del carioplasma, che aveva negli stadi precedenti; i filamenti cromatinici si individualizzano sempre più perdendo anche quei pseudoponti che presentano comunemente nei preparati istologici. Nel nucleo, a carioplasma anisto, si vengono a formare delle vescicole cromosomiche allungate di forma

VOL.
34
1953

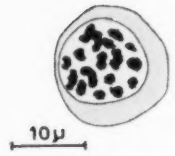

Fig. 6. Preoocita con cromosomi a vescicole. (Stadio corrispondente a quello della fig. 7). Color. emat. ferr.

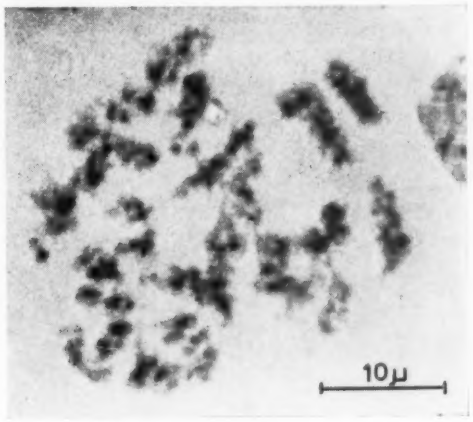

Fig. 7. Nucleo di preoocita a vescicole cromosomiche. Schiacc., color. emat. ferr.

irregolare (fig. 6). Nei preparati per schiacciamento questo tipo di struttura risulta molto evidente: i nuclei dei preoociti contengono delle vescicole, separate le une dalle altre, Feulgen-positive, che sembrano formate da una membrana (parte della matrice) e da filamento interno (cromatidio o cromatidi) avvolto ad elica. (Fig. 7.)

Nel passaggio da questo stadio a quello di preleptotene si ha una lieve contrazione del volume nucleare e la liberazione dei cromatidi dalle vescicole, così che il nucleo risulta infine completamente riempito da questi filamenti in via di svolgimento. Si possono trovare, sia nei preparati per sezioni che in quelli per schiacciamento, tutti gli stadi di passaggio di queste trasformazioni. Preoociti a vescicole cromosomiche eguali a queste sopradescritte, sono riferiti per gli stessi stadi dell'oogenesi, da MATTHEY (1945) in *Pycnoscelus suranimensis;* esatta mi sembra la sua ipotesi, che nei nuclei dei preoociti si individualizzano vescicole cromosomiche e da queste si rendono visibili i cromatidi che poi si liberano in seno al nucleo. Si può anzi precisare che si ha dapprima una contrazione dei cromosomi, probabilmente per contrazione della matrice e schiacciamento di un elicoide cromosomico (il cosidetto aumento di spiralizzazione), quindi si ha un dissolvimento della matrice, liberazione dei cromatidi e rilasciamento dell'elicoide per svolgimento, probabilmente fino alla scomparsa di alcuni degli avvolgimenti (coils).

Interessante è il confronto di queste trasformazioni nucleari dei preoociti con quelle dei prespermatociti. Nell'ultima telofase spermatogoniale il nucleo è pure formato da vescicole cromosomiche, queste però sono strettamente unite l'una all'altra e sembra che la loro matrice vada a formare la membrana nucleare. Nella serie femminile non è possibile identificare l'ultima divisione oogoniale, nei preoociti i cromosomi appaiono a vescicole di struttura identica

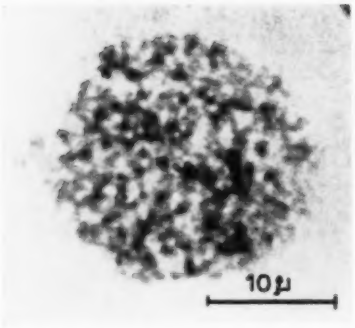

Fig. 8. Nucleo di occita preleptotenico. Schiacc., color. emat. ferr.

Fig. 9. Metafase oogoniale. Schiacc., color. emat. ferr.

VOL 34 195

a quelle dei prespermatociti; differiscono solo per il fatto che sono distanziati l'uno dall'altro in seno al nucleo. Lo svolgimento dei cromatidi avviene nelle due serie in maniera pressochè eguale e del tutto simili appaiono pure i nuclei preleptotenici degli spermatociti e degli oociti. (Fig. 8.)

Gli oociti di *Anacridium* dal preleptotene allo zigotene presentano sostanzialmente la stessa struttura nucleare degli spermatociti; si differenziano soltanto per la presenza in quest'ultimi dell'eterocromosoma. Questo si riesce a distinguere fin dall'ultima mitosi spermatogoniale per lo sfasamento della nucleinizzazione (secondo DARLINGTON 1937), e nella profase meiotica per il suo comportamento rispetto agli altri cromosomi cioè per essere nettamente eteropicnotico. Le fasi della spermatogenesi di *Anacridium* corrispondono esattamente a quelle descritte da DAVIS ancora nel 1908 per alcuni Acrididi americani.

Nelle metafasi oogoniali si contano invece 24 cromosomi tutti allo stesso grado di contrazione e di nucleinizzazione, eucromatici (fig. 9); allo zigotene si ha il numero aploide di bivalenti senza che, per la struttura, si possa distinguere uno dall'altro.

IV. LA STRUTTURA NUCLEARE E CROMOSOMICA NELLA PROFASE MEIOTICA.

La profase meiotica degli oociti di *Anacridium* si svolge complessivamente nel modo generalmente descritto per la maggior parte degli animali: nel nucleo si possono riconoscere facilmente gli stadi di leptotene e di zigotene; lo stadio di pachitene non è ben definibile, come del resto nella spermatogenesi, perchè si basa su caratteri cromosomici quanto mai relativi; nell'oogenesi dopo lo

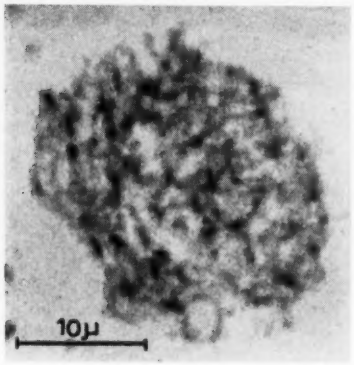

Fig. 10. Nucleo di oocita leptotenico. Schiacc., color. emat. ferr.

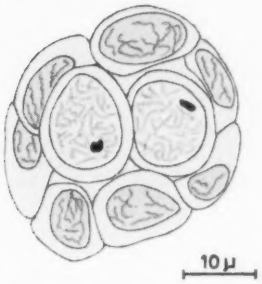

Fig. 11. Oociti in zigotene circondati dalle potenziali cellule follicolari. Sono evidenti anche i nucleoli. Color. emat. ferr.

VOL. 34 1953

zigotene si ha un enorme accrescimento nucleare e citoplasmatico con la scomparsa della visibilità dei cromosomi.

Nei preoociti a vescicole col precedere della differenziazione, come ho già riferito, si liberano in seno al nucleo i cromatidi o meglio i cromosomi veri e propri. Questi riempiono tutto il nucleo e presentano gli avvolgimenti telofasici ancora evidenti ma molto rilassati, i quali interessano tutto il corpo cromosomico. Questi avvolgimenti si vedono meglio nei preparati per sezione che in quelli per schiacciamento: nel complicato intreccio di filamenti cromatici che riempiono il nucleo si possono seguire tratti di cromosomi e veder porzioni dell'avvolgimento e si nota una rotazione del corpo cromosomico come si osserva frequentemente nelle profasi mitotiche.

Nel passaggio al leptotene i cromosomi parzialmente si raddrizzano, presentando solo in alcuni tratti, distribuiti irregolarmente lungo l'asse, un giro dell'avvolgimento; i filamenti appaiono ancora molto intrecciati tra loro così da rendere l'esame piuttosto difficile.

Nei preparati per schiacciamento, in cui l'esame della struttura nucleare riesce in genere più facile, i nuclei leptotenici risultano formati da filamenti ben distinti che riempiono completamente il nucleo e formano un intreccio complicato. (Fig. 10.)

Non ho mai visto contrazione della massa di cromosomi nè al centro nè verso un margine e neppure un orientamento dei filamenti. (Fig. 11.)

L'accoppiamento dei cromosomi, che porta allo zigotene, non è facilmente visibile, è tuttavia possibile vedere nei preparati per schiacciamento nuclei un po' più grandi di quelli leptotenici che presentano una parte del nucleo a filamenti radi ed un po' più grossi ed una parte con un intreccio di filamenti sottili e fitti. Questi sono evidentemente nuclei in cui è in atto la coniugazione degli omologhi.

Lo stadio di pachitene è riconoscibile meglio di tutti gli altri: nei preparati

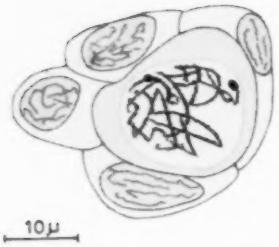

Fig. 12. Oocita in pachitene circondato da potenziali cellule follicolari. Sono stati disegnati anche i due nucleoli, che sembrano attaccati a due bivalenti od univalenti (?). Color. emat. ferr.

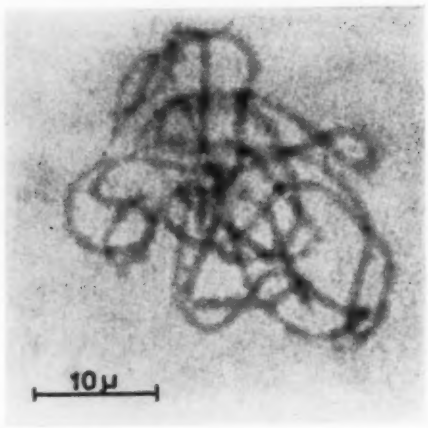

Fig. 13. Nucleo di oocita pachitenico. Schiacc., color. Feulgen.

per sezione i nuclei presentano nel loro interno i bivalenti, in numero aploide, relativamente spessi, ben distinguibili, perchè meno numerosi (fig. 12). Nei preparati per schiacciamento i nuclei pachitenici iniziali si distinguono dai leptotenici poichè presentano un intreccio meno fitto di cromosomi ed i filamenti sono più grossi. (Fig. 13.)

In stadi di pachitene un po' avanzato si ha un aumento del volume nucleare ed un ingrossamento dei bivalenti; questi appaiono però sempre unici, cioè i due omologhi accoppiati sono sempre strettamente uniti tra loro in modo che appare un nastro unico; talvolta però è possibile distinguere nell'interno di esso due filamenti paralleli più colorati.

Finchè i nuclei sono relativemente piccoli non si può vedere se i cromosomi si allungano o si accorciano; essi diventano più spessi ed appaiono a bordi spinosi con un aspetto simile a quello dei cromosomi pachitenici degli spermatociti. (Fig. 14.) Questo aspetto non ha niente a che vedere con i «lamp-brush chromosomes», che eventualmente si possono osservare in stadi molto più avanzati; si tratta di irregolarità dei bordi dei cromosomi, probabilmente dovute all'accollarsi ai cromatidi della matrice Feulgen-positiva, come del resto si vede talora anche in stadi molto precoci delle profasi mitotiche. Non vi è mai nei preparati per schiacciamento un quadro che possa far pensare a cromomeri; nei preparati per sezione invece è talora possibile accanto alla spinosità dei margini vedere lungo l'asse dei cromosomi degli ingrossamenti che assomigliano ai falsi cromomeri di WENRICH e che sono probabilmente giri dell'avvolgimento elicoidale.

Nei nuclei più grandi, cioè in pachitene più avanzato, i cromosomi diventano progressivamente più lunghi e più sottili (fig. 15). Per avere un'idea dell'allungamento ho eseguito alcune misure (riportate in micron) delle lunghezze

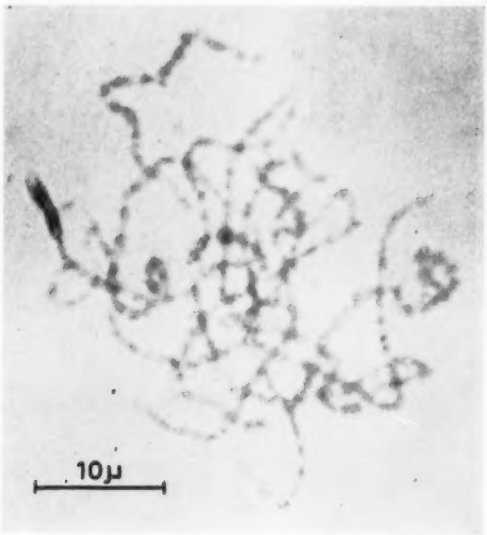

Fig. 14. Nucleo di oocita allo stadio di pachitene un po avanzato. Schiacc., color. Feulgen.

totali di tutti i cromosomi di alcuni nuclei su preparati per schiacciamento, ed ho trovato i seguenti valori: 281—282—309—325—351—397—460—465.

L'allungamento è in realtà ancora maggiore ma non è stato possibile misurarlo, perchè al pachitene precoce non si riesce a seguire tutti i filamenti

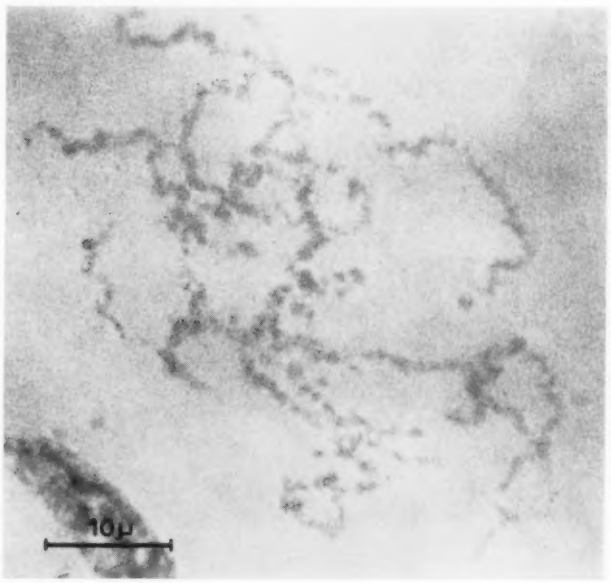

Fig. 15. Nucleo di oocita in postpachitene in cui i cromosomi stanno diventando sempre meno distinti. Schiacc., color. emat. ferr.

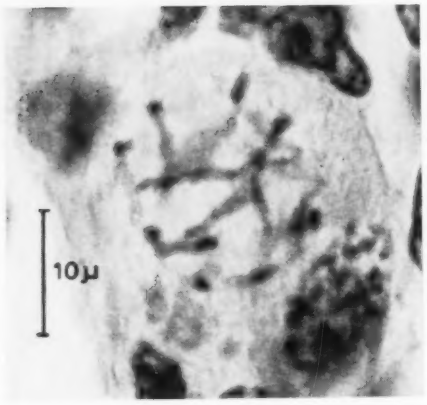

Fig. 16. Oocita allo stadio di pachitene un po' avanzato. E' visibile l'elicoide «maior» dei bivalenti. Fiss. Sanfelice; color. emat. ferr.

che formano un intreccio complicato ed al pachitene molto avanzato i cromosomi non si colorano più nettamente nè col metodo di Feulgen nè con l'ematossilina ferrica. Col metodo di Feulgen i filamenti cromosomici, al progredire dell'allungamento, appaiono sempre più sottili, ma omogenei, in alcuni casi mi è sembrato che si scompongano in due filamenti; anche colla colorazione all'ematossilina ferrica di Heidenhain, si può mettere in evidenza quest'assottigliamento dei cromosomi, che tuttavia presentano una struttura a bordi spinosi. (Fig. 15.)

Nelle fasi postpachiteniche si hanno delle modificazioni nucleari molto vistose che portano alla scomparsa della visibilità dei cromosomi. Il fatto più evidente è l'accrescimento del nucleo e la perdita della cromaticità.

Il quadro morfologico complessivo di questo processo in *Anacridium* non si discosta molto da quello descritto per esempio per gli Anfibi e per i Pesci (Carnoy e Lebrun, Ruckert, Marechal, Levi, e molto altri; tra i più resenti Dodson (1948). Le ricerche sulla struttura del nucleo degli oociti di

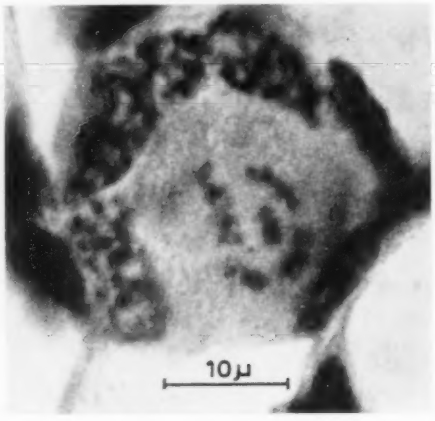

Fig. 17. Oocita alla stadio di postpachitene iniziale; i bivalenti mostrano evidenti la struttura ad avvolgimento ad elica: si tratta dello svolgimento dell'elicoide «minor» contemporaneamente allo scostamento cromosomico diplotenico. Fiss. Carnoy; color. emat. ferr.

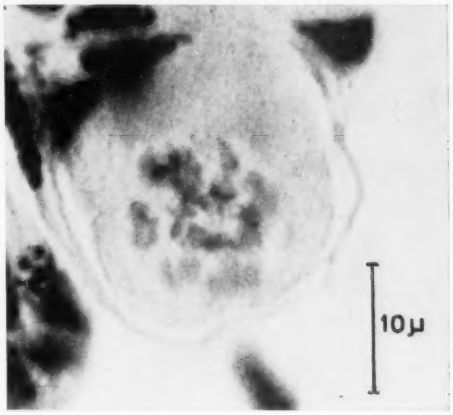

Fig. 18. Oocita allo stadio di postpachitene successivo a quello della fig. 17; i bivalenti mostrano la perdita della basofilia ed ulteriore svolgimento dell'elicoide «minor». Fiss. Carnoy; color. emat. ferr.

OL.
34
953

Anfibi, fatte con metodi sperimentali particolari, hanno dato un contributo notevolissimo alle nostre conoscenze sulla struttura nucleare e cromosomica (Durye 1950, Callan 1952).

Non sempre però tutti i materiali sono adatti per tale tipo di indagini ed in ogni caso un preciso studio morfologico fatto con le tecniche usuali è necessario prima di qualsiasi altro tipo di ricerca. Per questo motivo vengono qui descritte dettagliatamente le trasformazioni cromosomiche postpachiteniche, anche se osservate su preparati in un certo senso inadeguati; spero d'altronde che quanto prima saranno condotte a termine altre ricerche con tecniche più appropriate.

Nei preparati per sezione si vede che dal pachitene avanzato e negli stadi successivi i bivalenti perdono la loro forma a nastro od a cilindro apparentemente rigido, Feulgen-positivo, in cui sono eventualmente visibili nell'interno i due cromosomi omologhi e si rende visibile la struttura elicoidale (fig. 16). I giri dell'avvolgimento si osservano prima a livello dei nodi ingrossati dei bivalenti pachitenici, come ho già descritto, e poi si estendono a tutta la lunghezza del bivalente, che a sua volta presenta un andamento elicoidale proprio. In un secondo tempo si rendono ben distinti i due cromosomi, ciascuno con un avvolgimento proprio e strettamente accostati, così che il bivalente ha apparentemente un aspetto vacuolizzato (fig. 17 e 18). Questi apparenti vacuoli corrispondono ai punti in cui i due cromosomi sono più distanziati; nelle proiezioni del pezzo trasversale dell'avvolgimento essi appaiono strettamente uniti.

La comparsa di questo tipo di avvolgimento non è altro che una tappa del rilassamento dei cromosomi; infatti nelle ulteriori trasformazioni i bivalenti appaiono come masse ben delimitate, di forma fissa, formate da filamenti sottili avvolti ed intrecciati tra loro in maniera complicata. (Fig. 19.)

A questo stadio la forma dei bivalenti ricorda le figure diploteniche, si osservano degli anelli, degli X, però i cromosomi presentano un aspetto sfumato ed irregolare, perchè appunto risultano a loro volta scomposti in filamenti

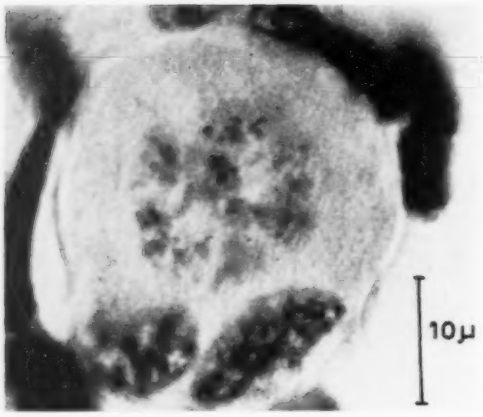

Fig. 19. Oocita allo stadio di postpachitene successivo a quello della fig. 18. Fiss. Carnoy; color. emat. ferr.

VOL. 34 1953

sottili e complicati, circondati od immersi in una massa di sostanza non ben definibile, che si colora coi coloranti acidi.

I bivalenti fino a questo stadio si colorano col metodo di Feulgen, benchè non così nettamente come i cromosomi leptotenici e pachitenici, (si colorano contemporaneamente col verde luce); precisamente sono Feulgen-positivi sottili filamenti che si trovano immersi in seno ad una massa strutturalmente assai mal definibile, che dà la forma alle diadi.

Col procedere dell'accrescimento nucleare le figure dei bivalenti si allungano, perdono un po' la loro individualità ed in esse si vedono dei filamenti Feulgen-positivi sempre più lunghi e sempre più sottili, disposti piuttosto irregolarmente a zigzag ed intrecciati tra loro. (Fig. 20.)

Successivamente tali filamenti non sono più visibili; col metodo di Feulgen unito a una colorazione di contrasto (verde luce) il nucleo appare completamente vuoto ed uniforme.

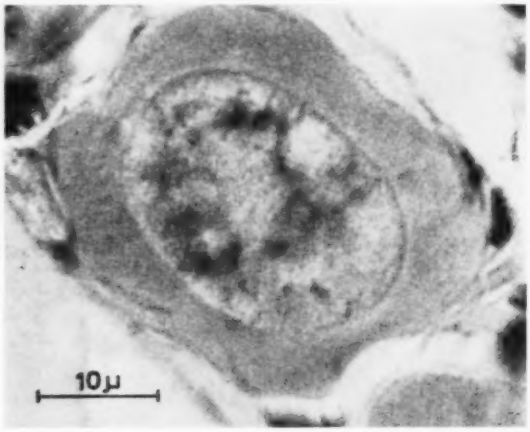

Fig. 20. Oocita in postpachitene avanzato in cui i bivalenti sono ancora confusamente visibili. Fiss. Carnoy; color. emat. ferr.

Tale aspetto si osserva nei preparati fissati con tutti i diversi liquidi usati. Colla colorazione col metodo Unna-Pappenheim il nucleo, dopo che i cromosomi non sono più visibili, appare vuoto od al massimo costituito da un reticolo di filamenti debolmente colorati.

Con la colorazione all'ematossilina ferrica di Heidenhain il nucleo appare fondalmentalmente formato da sottili filamenti; si possono vedere però degli addensamenti leggermente colorati di forma allungata, che corrispondono ai bivalenti.

A fresco questi nuclei esaminati appena allestito il preparato appaiono otticamente vuoti ed omogenei, salvo che per l'apparato siderofilo che verrà descritto più avanti.

Se si esaminano (col microscopio a contrasto di fase) gli stessi preparati a fresco in olio di vaselina, più di 6 ore dopo che sono stati allestiti, è possibile intravedere nei nuclei, prima otticamente vuoti, dei filamenti sottili e lunghi dal cui asse si staccano ad angolo retto altri filamenti piuttosto corti: un quadro del tutto simile a quello descritto per i cromosomi a spazzola o «lampbrush chromosomes» degli Anfibi da DURYEE e da CALLAN. I cromosomi a spazzola, anche se nei preparati istologici non si vedono, effettivamente ci sono.

Un quadro esatto della struttura nucleare nel postpachitene avanzato non è ancora possibile; basarsi su preparati inadeguati è inutile; le ricerche ulteriori potranno darci delle informazioni esatte. Tuttavia si può già cercare di ricostruire la serie delle modificazioni cromosomiche cominciando dal preleptotene.

Tutte le variazioni della struttura cromosomica sopra descritte possono, in linea generale, essere ricondotte ad avvolgimenti o svolgimenti degli elicoidi cromosomici e cromonemici secondo l'interpretazione di DARLINGTON (1937). (Il termine «spirale» e «spiralizzazione», ormai entrato nell'uso comune in cariologia, va evitato perchè non corrisponde alla esatta figura geometrica degli avvolgimenti cromosomici).

Dall'interfase oogoniale al leptotene si avrebbe lo svolgimento delle due elicoidi *super* e *maior*, secondo la nomenclature e lo schema di CLEVELAND (1949); la *minor* rimane nei cromosomi leptotenici e dovrebbe rimanere anche nel corso della coniugazione cromosomica che porta allo zigotene. Le successive trasformazioni cromosomiche postzigoteniche sono più difficili da interpretare e, secondo lo schema adottato, consisterebbero nello svolgimento anche della *minor*, per cui nei cromosomi a spazzola si avrebbero i filamenti cromonemici stesi.

Tale interpretazione derivata dall'esame del processo di trasformazione dei cromosomi, è certamente discutibile ed un confronto con stadi corrispondenti dell'oogenesi di altri animali non è possibile, perchè è difficile determinare la corrispondenza di stadi. Essa è più che altro un'ipotesi di lavoro, che va controllata con altre ricerche; metterebbe però d'accordo le opinioni di RIS e di DURYEE sull'argomento. Infatti, da quanto io ho inteso dalle descrizioni ri-

portate nei lavori dei suddetti Autori, probabilmente Ris si riferisce molto spesso ai cromosomi postpachitenici iniziali in cui è presente ancora l'elicoide *minor*, mentre lo schema cromosomico di Duryee si riferisce ai cromosomi di nuclei allo stadio di postpachitene molto avanzato in cui lo svolgimento della *minor* sarebbe completo.

Più difficile è invece la comparazione tra il comportamento cromosomico in fasi corrispondenti della meiosi spermatogenetica e di quella oogenetica. Negli stadi comparabili (leptotene e pachitene) la struttura dei cromosomi degli spermatociti e degli oociti è identica però nella spermatogenesi i cromosomi si allungano nel leptotene e si accorciano nello zigotene e pachitene; nell'oogenesi si avrebbe un allungamento progressivo che non si ferma al pachitene ma continua nel postpachitene.

Probabilmente nella meiosi maschile i cambiamenti strutturali dei cromosomi interessano soltanto gli avvolgimenti *super* e *maior*, in quella femminile si svolge anche la *minor*.

La lunghezza totale del complesso cromosomico allo zigotene, limitatamente alle misure che è stato possibile eseguire, è pressochè eguale nella serie maschile e nella serie femminile: circa 400 μ (vedi sopra) per gli oociti e pure circa 400 μ per gli spermatociti (vedi Colombo 1952).

Tuttavia l'esatto comportamento cromosomico potrà essere chiarito, non tanto dalle misure e dall'esame delle strutture microscopiche, quanto da una più approfondita conoscenza della struttura submicroscopica dei cromosomi mitotici e meiotici.

V. L'APPARATO SIDEROFILO (ENDONUCLEARE).

Colla scomparsa della visibilità dei bivalenti, nei nuclei degli oociti si sviluppa una formazione siderofila endonucleare che probabilmente è un'aspetto dell'apparato nucleolare.

Negli oogoni e nei preoociti di *Anacridium* non sono mai riuscito a vedere nucleoli; allo stadio di leptotene si trovano generalmente uno o due nucleoli acidofili sferici che si colorano col verde luce e con l'ematossilina ferrica e con

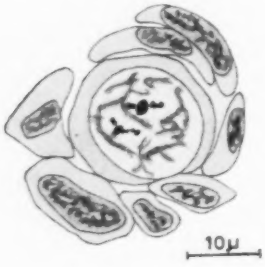

Fig. 21. Oocita in postpachitene iniziale circondato dalle potenziali cellule follicolari. Nel nucleo sta formandosi dai nucleoli l'apparato siderofilo. Color. emat. ferr.

VOL. 34 1953

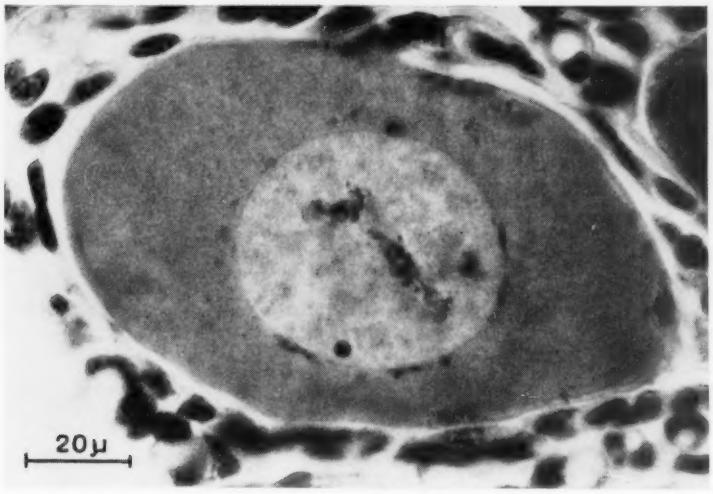

Fig. 22. Oocita in 2° periodo di accrescimento. E' evidente nel nucleo l'apparato siderofilio; granuli siderofili si vedono anche attorno alla membrana nucleare. Fiss. Sanfelice; color. emat. ferr.

la pironina. Nei preparati colorati col metodo di Feulgen e col verde luce questi nucleoli sono visibile anche nello stadio di pachitene e nel postpachitene iniziale, sono sempre colorati in verde e talora allo zigotene sono anche debolmente Feulgen-positivi. Nelle prime fasi del postpachitene essi si accrescono molto (2 e anche 3 volte), rimanendo sferici, nel postpachitene avanzato appaiono allungati e di forma irregolare. Il loro esame riesce molto difficile perchè col procedere dell'accrescimento si colorano sempre più debolmente col verde luce, o meglio il nucleo si colora uniformemente col verde luce cosicchè non si distingue alcuna struttura intranucleare. Nei preparati colorati con l'ematossilina ferrica, allo stadio di leptotene si vedono in genere due nucleoli ben delimitati, ed inoltre una o due vescicole piuttosto piccole, pure colorate con l'ematossilina, attaccate a filamenti cromosomici. Allo stadio di zigotene nel nucleo si vedono due nucleoli sferici od ovoidali, piuttosto grandi. (Fig. 11.)

Nella nota preliminare, già pubblicata, avevo segnalato queste formazioni interpretandole come parti eterocromatiche degli omologhi XX, perchè mi sembravano appaiate e poste nella parte terminale di un bivalente. Ad un riesame dei preparati non sono riuscito a decidere quale sia l'esatta interpretazione di queste strutture, cioè se si tratti di due nucleoli o di parti eterocromatiche di una coppia cromosomica oppure se vi siano tutte e due le formazioni contemporaneamente; nei preparati per schiacciamento, anche se colorati con l'ematossilina ferrica, i nuclei leptotenici e pachitenici non presentano nè nucleoli nè parti eterocromatiche.

Nei preparati per sezione colorati con l'ematossilina ferrica, nei nuclei postpachitenici, quando i cromosomi stanno perdendo la cromaticità, i due nucleoli,

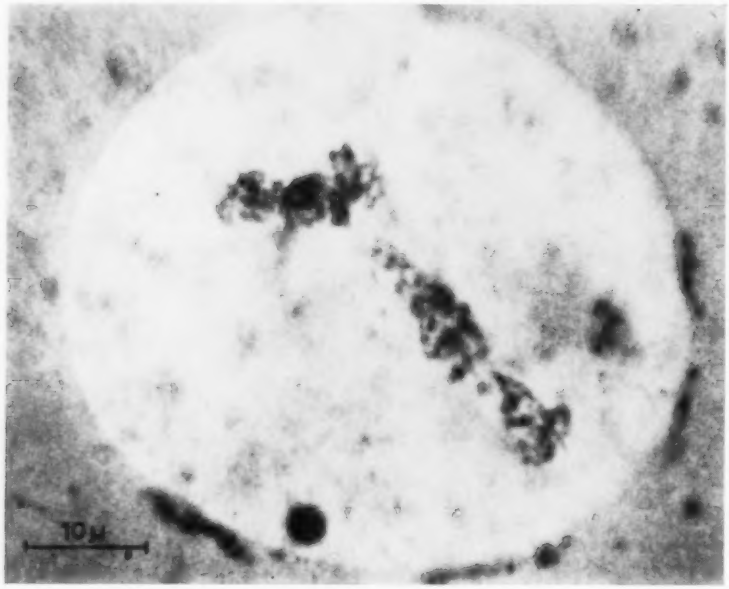

Fig. 23. Nucleo dell' oocita della fig. 22.

che si vedono negli stadi precedenti, si moltiplicano e si formano dei piccoli nucleoli, prima in numero di uno o due, poi molto numerosi che si dispongono uno di seguito all'altro. (Fig. 21.) Di solito questi nucleoli si trovano accostati a dei bivalenti che stanno scomparendo, però non è possibile vedere quale rapporto vi sia fra loro.

Col procedere dell'accrescimento oocitario questo apparato nucleolare assume uno sviluppo grandissimo; si vedono sioè nei nuclei, fondamentalmente costituiti da un intreccio di filamenti debolmente colorabili, due ammassi di piccole formazioni sferiche intensamente colorate coll'ematossilina ferrica, poste in fila e unite l'una all'altra da un filamento piuttosto spesso, pure colorato con l'ematossilina ferrica. Si vedono cioè in complesso due filamenti moniliformi ciascuno dei quali è disposto ad anse ravvicinate e strettamente accostate lungo una linea centrale; spesso nelle sezioni alcune anse appaiono spostate senza ordine in seno al nucleo. (Fig. 22, 23, 24, 25, 26.) Sembrerebbe si trattasse di un cromosoma eterocromatico, molto lungo che produca nucleoli.

Colla colorazione Unna-Pappenheim questa formazione si colora in rosso (colla pironina); negli oociti pachitenici si distinguono dei veri e propri nucleoli, uno o due più grossi con attorno due o tre più piccoli, negli oociti più grandi si notano invece una o due masse allungate e di forma irregolare colorate in rosa; lo stesso quadro si ha con la colorazione col cresil-violetto.

Con questi coloranti specifici per le ribonucleo-proteine non si vedono le

VOL.
34
1953

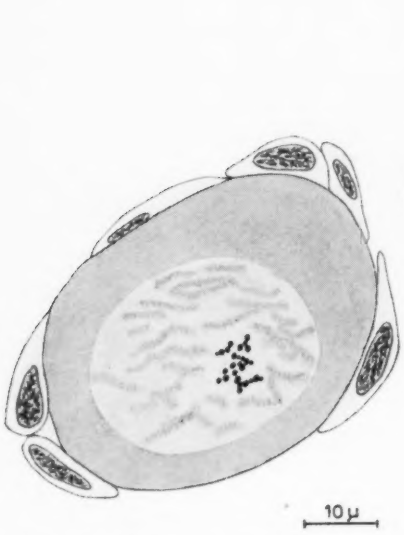

Fig. 24. Oocita in 2° periodo di accrescimento. L'apparato siderofilo in via di sviluppo. Color. emat. ferr.

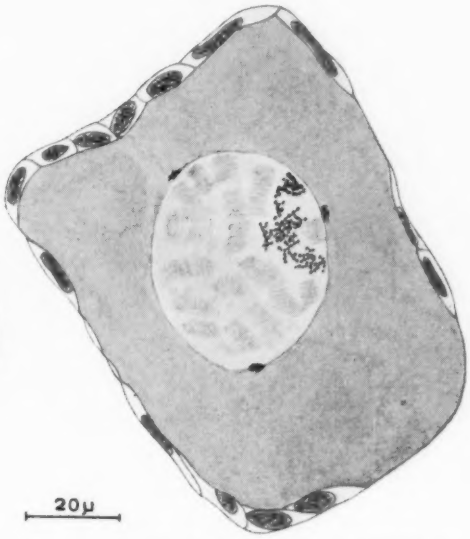

Fig. 25. Oocita in pieno secondo periodo accrescimento con l'apparato siderofilo ben sviluppato. Color. emat. ferr.

particolarità strutturali che si mettono in evidenza soltantto con la colorazione coll'ematossilina ferrica di Heidenhain.

All'esame a fresco i nuclei, come ho detto sopra, appaiono otticamente vuoti; si vedono invece ben distintamente due formazioni intranucleari, che appaiono come un cordone avvolto ad elica presentante lungo tutto il decorso degli ingrossamenti sferoidali: il tutto corrisponde all'apparato che si vede nei preparati fissati (fig. 27).

Si può concludere perciò che questi corpi siderofili sono proprio delle formazioni nastriformi con una struttura propria, quale è stata descritta, e che si può vedere facilmente anche a fresco: la cosa più semplice da pensare è che siano dei cromosomi i quali hanno una funzione particolare nell'oogenesi simile a quella svolta dai nucleoli, e che si comportano parzialmente in maniera eterocromatica.

Lo sviluppo maggiore di questo apparato siderofilo coincide con l'attivo accrescimento oocitario ed è contemporaneo alla comparsa di granulazioni e di piccole masse di sostanza colorabile soltanto con l'ematossilina ferrica, poste a ridosso della membrana nucleare e talora sporgenti nel citoplasma.

L'ulteriore destino della struttura suddetta non è stato ancora esaminato completamente perchè non ho ancora il materiale sufficiente per descrivere tutta la serie delle trasformazioni dell'oocita da questo stadio a quello di uovo pronto per la deposizione.

Buchner (1909) ha descritto in *Gryllus* la presenza di una formazione cro-

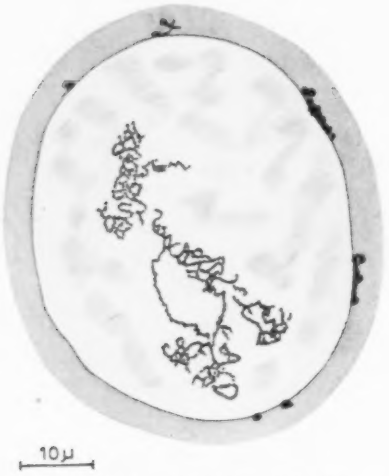

Fig. 26. Nucleo dell'oocita delle fig. 22 e 23, in cui è stato disegnato nello stesso piano tutto lo sviluppo dell'apparato siderofilo.

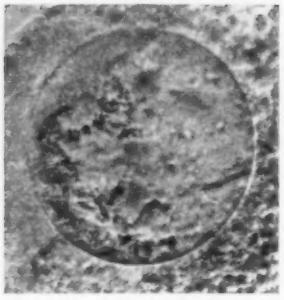

Fig. 27. Nucleo di oocita in 2° periodo di accrescimento osservato a fresco a contrasto di fase. Ingr. 750 circa.

VOL. 34 1953

matica, che, almeno dalle figure, assomiglia a quella dell'*Anacridium*, benchè i particolari strutturali riportati da BUCHNER non siano molto precisi e non siano confermati da osservazioni a fresco. In *Gryllus* questo corpo accessorio si trova già negli oogoni (BUCHNER) ed avrebbe un comportamento simile alla massa del GIARDINA negli oogoni di *Dytiscus;* si tratterebbe di un vero e proprio cromosoma sopranumerario, come si trova negli spermatociti il quale funziona da determinante germinale nell'oogenesi.

In *Anacridium*, come ho più volte sopradescritto, l'eterocromosoma si vede solo nella serie maschile, e con un comportamento simile a quello della maggior parte degli Acrididi. Non si può escludere tuttavia che alcuni cromosomi delle cellule germinali femminili non posseggano parti eterocromatiche che manifestino delle differenze morfologiche durante l'oogenesi.

JÖRGENSEN (1913) nel suo ampio lavoro sull'accrescimento nucleare riporta alcune osservazioni su nuclei di oociti in accrescimento di Ortotteroidi. La disposizione dei nucleioli saffraninofili di *Decticus* assomiglia molto nella forma complessiva all'apparato siderofilo di *Anacridium*.

In questo, a parer mio, in base sopratutto alle osservazioni a fresco, si tratta probabilmente di due cromosomi in cui la parte eterocromatica ha uno sviluppo morfologico e funzionale preponderante. Resta da esaminare quale relazione ci sia tra questi e gli eucromosomi e sopratutto se si tratti di bivalenti o di univalenti. Al leptotene ed allo zigotene tutti i cromosomi sono eucromatici e non si possono distinguere l'uno dall'altro, è presumibile quindi che tutti si accoppino. Se si ammette che l'apparato siderofilo consista di due univalenti,

questi si disgiungerebbero nel postpachitene e diventerebbero eterocromatici; ammettendo invece che si tratti di due bivalenti sorgono delle difficoltà esaminando la loro formazione; i due corpi siderofili derivano chiaramente da due nucleoli che sono ben visibili al leptotene ed allo zigotene; è altresì improbabile che due nucleoli siano associati a singoli cromosomi di due coppie diverse.

Le osservazioni morfologiche, qui fatte, saranno completate in un prossimo lavoro da osservazioni istochimiche per chiarire la natura di questo apparato endonucleare; rimandando alla nota successiva una più ampia discussione, si può tuttavia senz'altro ammettere che si tratti di un apparato di tipo nucleolare.

VI. L'ACCRESCIMENTO OOCITARIO.

La differenza più vistosa tra oogenesi e spermatogenesi sta nel fatto che nella oogenesi si ha un enorme aumento volumetrico degli ovociti.

Per *Anacridium*, come per *Carausius* (PEHANI) (1925) e *Saga pedo* (MATTHEY) (1925) l'accrescimento oocitario può essere diviso: (a) in un primo periodo di accrescimento o piccolo accrescimento, che comprende l'aumento volumetrico che comincia con la differenziazione oocitaria e va fino al zigotene; (b) un secondo periodo di accrescimento che avviene nel postzigotene quando i cromosomi non sono più visibili e (c) un terzo periodo o maturazione dell'uovo che si attua con la vitellogenesi. Questa divisione corrisponde a quella che viene adottata nell'oogenesi dei Vertebrati (per gli Anfibi vedi tra gli Autori recenti GALGANO (1945); essa può essere estesa a tutti gli Insetti anche perchè i processi fisiologici che vi intervengono (vedi sopra) sono in certo senso simili nei vari gruppi.

I processi citologici che regolano l'accrescimento ovocitario sono pure, per molti punti di vista, simili per tutti gli animali e su tale criterio si basa la rassegna comparativa sull'oogenesi di JÖRGENSEN (1913). Una tale comparazione potrebbe essere rifatta, perchè molto più estese sono le nostre conoscenze sulla fisiologia cellulare, però un riesame dei processi oogenetici nei vari gruppi animali, con tecniche moderne, è ben lontano dall'essere sufficientemente esteso. Tuttavia l'interpretazione delle ricerche più antiche (cfr. WILSON (1937)), pur eseguite con tecniche inadeguate, anche se non è esatta sotto certi punti di vista particolari, è stata in linea generale confermata dalle ricerche più recenti. (COTRONEI, URBANI, HUGHES—SCHRADER, ecc.)

Dal punto di vista morfologico la divisione dell'accrescimento oocitario in tre periodi viene fatta in base alle variazioni della struttura nucleare ed in molti casi in base alla caratteristiche del citoplasma, come per es. aumento della basofilia, o allo sviluppo dell'apparato nucleolare (tra le ricerche recenti vedi VANNINI 1950) o di altre strutture paranucleari (pure lavori recenti, vedi URBANI 1949).

In *Anacridium* le modificazioni della struttura nucleare corrispondono ai diversi stadi dell'accrescimento; invece non è stato possibile, con le tecniche usate, mettere in evidenza variazioni della basofilia citoplasmatica, nè la presenza di strutture citoplasmatiche simili a quelle citate da GIARDINA (1902) per gli oociti di *Mantis*. Nel primo e nel secondo periodo di accrescimento il citoplasma degli oociti (fissati) di *Anacridium* presenta sempre una struttura finemente granulare ed omogenea e la basofilia aumenta lievemente all'inizio del secondo periodo di accrescimento, ma rimane costante; colla colorazione Unna-Pappenheim al verde di metile-pironina si trova sempre il citoplasma tinto in rosa pallido.

Un'analisi delle caratteristiche istochimiche degli oociti in accrescimento è in corso, ma non è stata ancora compiuta, e nelle ricerche che si trovano in letteratura, sull'argomento, (NATH e MOHAN, PAINE, ed altri), benchè vi siano dei dati molto interessanti, non sono mai riportate le variazioni nel corso dell'accrescimento.

VOL.
34
1953

Una prima analisi dei processi di accrescimento è stata fatta dal punto di vista citometrico cioè analizzando le variazioni volumetriche, nucleari e citoplasmatiche nel corso dell'oogenesi. Per i primi stadi, fino al postpachitene, sono stati misurati gli oociti ed i loro nuclei su preparati per sezione, adoperando un solo preparato (ovario di larva al 3° stadio, fissazione Sanfelice, colorazione di Feulgen) per evitare le variazioni dovute a trattamenti diversi (misure su preparati diversi hanno mostrato delle differenze notevoli). Naturalmente non è possibile evitare la diversa contrazione, di fronte alle soluzioni dei fissativi, delle cellule a diverso stato funzionale. Sono state misurate cellule la cui sezione maggiore era presumibilmente contenuta nella sezione; ciò è possibile, al microscopio, fochettando e scegliendo le cellule in cui il nucleo e il citoplasma diminuiscono di diametro sia nel piano superiore che inferiore del preparato.

Oogoni ed oociti a stadi ben definiti sono stati disegnati ad ingrandimenti noti con l'aiuto della camera chiara (LEITZ); sulle figure sono stati misurati i due diametri ortogonali, uno dei quati il massimo. Da queste misure sono stati calcolati i volumi secondo la formula $A \times B \times \frac{A \times B}{2} \times \frac{\pi}{6}$ considerando cioè le cellule ed i nuclei come elissoidi con gli assi A, B ed il terzo asse medio tra i due. Il volume del citoplasma è stato ricavato come differenza tra il volume totale ed il volume del nucleo. Non sono stati misurati molti elementi, preferendo essere sicuro che si trattasse di cellule a diametro massimo ed a stadio noto e tutti rilevati da uno stesso preparato. I valori trovati, espressi in μ^3, unitamente alla media del rapporto nucleo-plasmatico per ciascun gruppo di cellule, sono riportati nella seguente tabella.

Per dare una visione grafica dell'andamento è stato costruito il diagramma 1 in cui sulle ascisse sono segnati, a distanza arbitraria ed eguale, gli stadi di differenziazione e sulle ordinate le medie dei volumi con la deviazione standard.

Tipi di cellule	Numero dei nucl. misurati		Volume totale	Volume dei nuclei	Volume del citoplasma	Rapporto nucleo-plasmatico
Oogoni isolati	4	$\bar{x}$	499	209	289	0.413
		s	88	84	29	
		$s_{\bar{x}}$	44	42	15	
Preoociti	6	$\bar{x}$	751	205	546	0.282
		s	198	72	154	
		$s_{\bar{x}}$	81	30	64	
Preleptotene	9	$\bar{x}$	1054	329	725	0.310
		s	229	145	174	
		$s_{\bar{x}}$	77	49	58	
Leptotene	8	$\bar{x}$	1623	475	1147	0.310
		s	414	165	389	
		$s_{\bar{x}}$	47	59	138	
Pachitene	6	$\bar{x}$	2614	937	1677	0.353
		s	577	264	261	
		$s_{\bar{x}}$	236	108	107	
Postpachitene iniziale . .	8	$\bar{x}$	10482	2834	7648	0.265
		s	2280	1010	1460	
		$s_{\bar{x}}$	804	355	516	

$\bar{x}$ = media; s = deviazione standard; $s_{\bar{x}}$ = errore standard.

Dalla tabella e dal grafico si vede che l'accrescimento cellulare si inizia colla differenziazione degli oogoni in oociti; questi poi aumentano di volume in modo notevole col procedere della meiosi.

Considerando separatamente l'accrescimento del nucleo e quello del citoplasma, si vede che l'accrescimento citoplasmatico comincia col differenziarsi dei preoociti; continua pressochè con lo stesso ritmo fino al pachitene, in seguito presenta un incremento grandissimo. Il nucleo comincia ad accrescersi all'inizio della profase meiotica al preleptotene, diventa doppio al leptotene e si raddoppia ancora al pachitene.

Se consideriamo il passaggio da stadio a stadio corrispondente al tempo, si vede che l'accrescimento considerato è una funzione iperbolica analoga a quella che si trova in generale in tutti i processi biologici di accrescimento.

Per gli stadi qui considerati è possibile confrontare il comportamento degli oociti con quello degli spermatociti.

Per quanto riguarda il nucleo, nella tabella sottoriportata sono indicate le medie dei valori assoluti dei volumi nucleari di stadi corrispondenti dell'oogenesi e della spermatogenesi di *Anacridium* (per la spermatogenesi sono state adoperate le misure riferite in una mia nota precedente) (COLOMBO 1951).

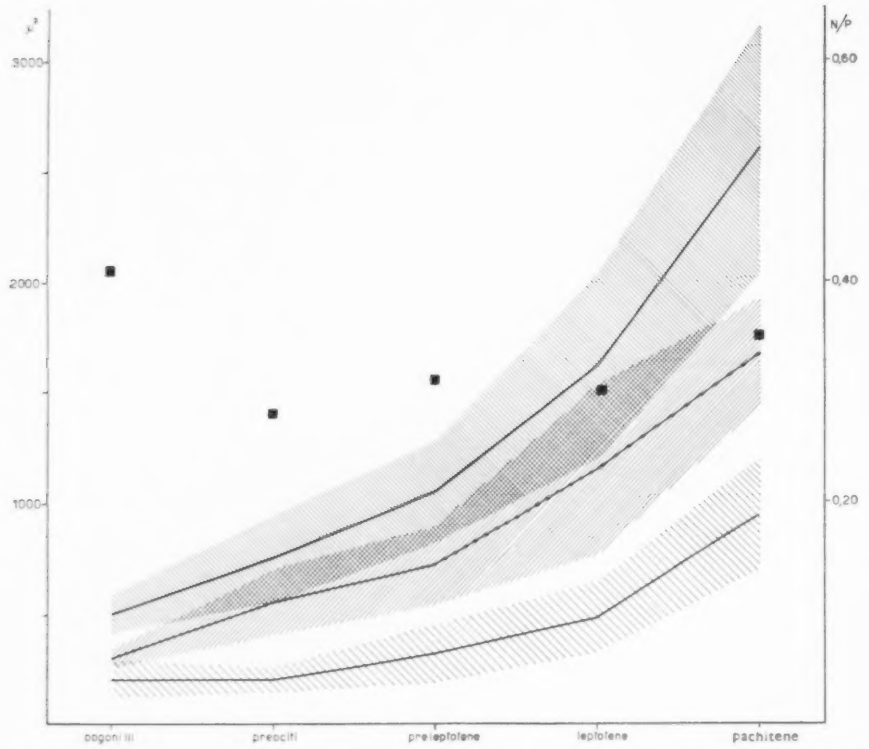

Diagramma 1. Curve dell'accrescimento volumetrico da oogoni ad oociti pachitenici e variazioni del rapporto nucleo-plasmatico, ricavate dalla tabella 1. Sulle ascisse sono indicati gli stadi, sulle ordinate a sinistra i volumi in μ^3, sulle ordinate a destra i valori del rapporto nucleoplasmatico. Le spezzate indicano le medie, l'ampiezza delle fascie la deviazione standard. La curva superiore si riferisce all'accrescimento totale, quella intermedia all'accrescimento citoplasmatico, quella inferiore all'accrescimento nucleare. I quadrati pieni indicano il valore del rapporto N/P per ciascuno stadio.

Volumi nucleari in μ^3 (.)

	Oociti	*Spermatociti*
Preleptotene	329	376
	(6)	(64)
Leptotene	475	492
	(8)	(71)
Pachitene iniziale	937	962
	(6)	(116)
Postpachitene (..) (pachitene)	1 373	1 204
	(6)	(249)

(.) Tra parentesi è indicato il numero di nuclei misurato.

(..) Per lo stadio di postpachitene degli oociti è stato preso quello dei nuclei all'inizio della trasformazione cromosomica che presentano i cromosomi ancora ben visibili ma non più di aspetto zigotenico, stadio che si può considerare corrispondente al pachitene degli spermatociti, benchè sia in realtà molto diverso.

VOL.
34
1953

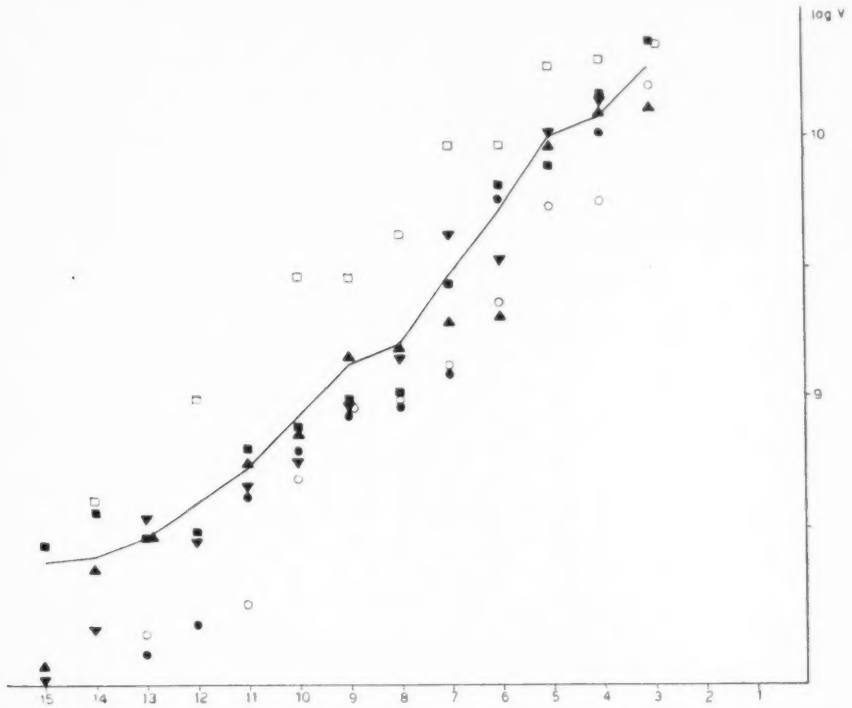

Diagramma 2. Curva di accrescimento degli oociti. Sulle ascisse è indicata la successione degli oociti negli ovarioli cominciando dall'ovidotto (o) al germario (15); sulle ordinate sono indicati i logaritmi dei volumi. I segni eguali si riferiscono ad oociti di uno stesso ovariolo, tutti di un medesimo ovario.

La concordanza dei valori è evidente.

L'accrescimento citoplasmatico nella serie maschile e femminile è più difficilmente comparabile perchè il citoplasma negli spermatociti è molto ridotto e non si può facilmente misurare. Osservazioni non pubblicate, perchè solo di valore indicativo ed approssimato, dei primi stadi della profase meiotica maschile in *Anacridium*, mostrano che dal preleptotene al pachitene assieme all'aumento notevole del volume cellulare, il rapporto nucleo-plasmatico, diminuisce; ciò indica che l'accrescimento volumetrico del citoplasma è maggiore di quello del nucleo; ma rimane sempre entro variazioni modiche.

Il significato di quanto è sopra esposto non è di semplice interpretazione; la concordanza delle variazioni volumetriche nucleari, fino al pachitene degli spermatociti ed al postpachitene iniziale degli oociti, dimostrerebbe che fino a quello stadio i processi che si succedono nel nucleo sono identici, e legati alla autoriproduzione dei cromosomi e principalmente ai cambiamenti della struttura del nucleo nella meiosi eguali nelle cellule maschili e femminili.

Le variazioni volumetriche del citoplasma sono pure simili nei primi stadi ed

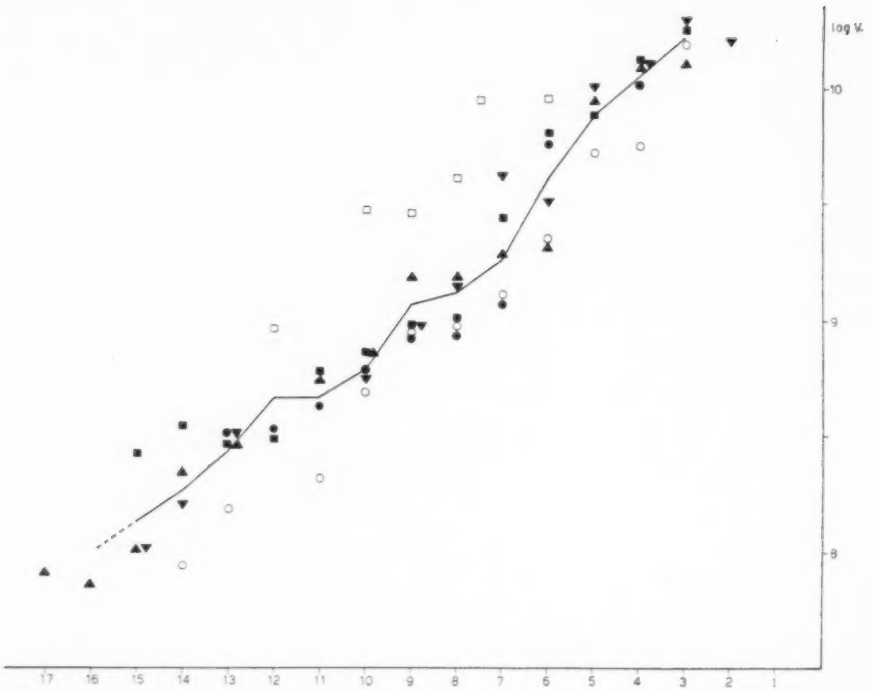

Diagramma 3. Curva di accrescimento del citoplasma degli stessi oociti dei diagramma 2.

indicano una corrispondenza di processi in relazione al comportamento nucleare; al pachitene poi comincia la sintesi delle sostanze nel citoplasma degli oociti per cui in questi al primo accrescimento citoplasmatico si aggiunge un secondo accrescimento, che raggiunge un suo massimo negli stadi compresi nel postpachitene per accumulo di sostanze, regolato dal nucleo (2° periodo di accrescimento). Quest'ultimo processo non si verifica negli spermatociti.

Come ho sopra accennato, occiti in secondo periodo di accrescimento si trovano negli ovari delle larve negli ultimi stadi larvali e delle imagini poco tempo dopo l'ultima muta; in queste è anzi possibile esaminare gli ovarioli a fresco e misurare gli oociti in stadi successivi di accrescimento dal postpachitene all'inizio della vitellogenesi.

Ho perciò misurato con un oculare micrometrico i diametri cellulari e nucleari degli oociti su preparati a fresco e calcolati i volumi secondo la formula dell'elissoide. Poichè la successione topografica corrisponde all'età relativa degli oociti, ho costruito i diagrammi seguenti in cui sulle ascisse è segnato, a distanza eguale, l'ordine in cui si trovano gli oociti cominciando dall'ovidotto fino al germario; sulle ordinate i volumi cellulari, nucleari e citoplasmatici espressi in logaritmi per poter contenere nei diagrammi anche i valori più alti.

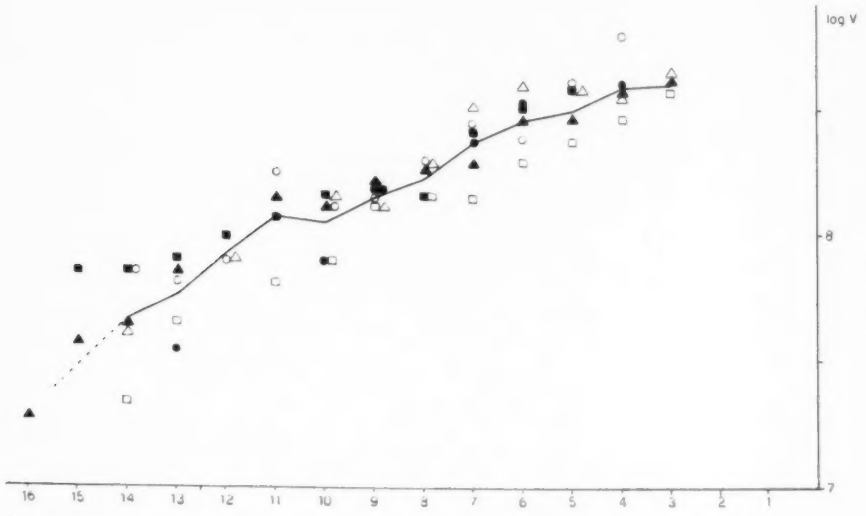

Diagramma 4. Curva di accrescimento del nucleo degli stessi oociti del diagramma 2.

I valori sono distribuiti approssimativamente secondo una retta il che indica che forse la curva di accrescimento esprime una funzione iperbolica con il tempo come variabile. Poichè la distribuzione topografica degli ovociti lungo l'ovariolo rappresenta anche l'età relativa, i valori sulle ascisse si possono considerare approssimativamente corrispondenti al tempo. (Diagrammi 2, 3, 4.)

Se si esaminano contemporaneamente i tre grafici si vede che l'accrescimento complessivo è dovuto principalmente all'aumento del citoplasma.

Le linee che indicano l'accrescimento nucleare, citoplasmatico e degli oociti interi presentano tutte una inflessione tra gli oociti 7 e 9. Negli ovarioli misurati e riportati nel grafico, proprio in quella posizione si incominciano a vedere oociti con granulazioni di tuorlo nel citoplasma, cioè all'inizio della vitellogenesi, ed al medesimo livello si ha un diverso ritmo di accrescimento rilevabile citometricamente.

Esaminando l'accrescimento complessivo degli oociti nei tre periodi si può pensare che la curva generale di accrescimento sia composta di tre curve che si succedono l'una all'altra ed in cui il valore massimo raggiunto dalla precedente è il punto di partenza della successiva. Ammettendo che ciascun periodo di accrescimento possa essere rappresentato da una curva, sigmoide, come è probabile, l'accrescimento degli oociti può essere espresso come nel diagramma 5, in cui in base alle osservazioni sono stati determinati i punti più caratteristici per ogni periodo di accrescimento o da questi sono state disegnate le curve il cui andamento è stato desunto dalle osservazioni su riferite.

L'accrescimento volumetrico degli oociti rappresenta un caso particolare delle variazioni volumetriche generali delle cellule e dei suoi costituenti.

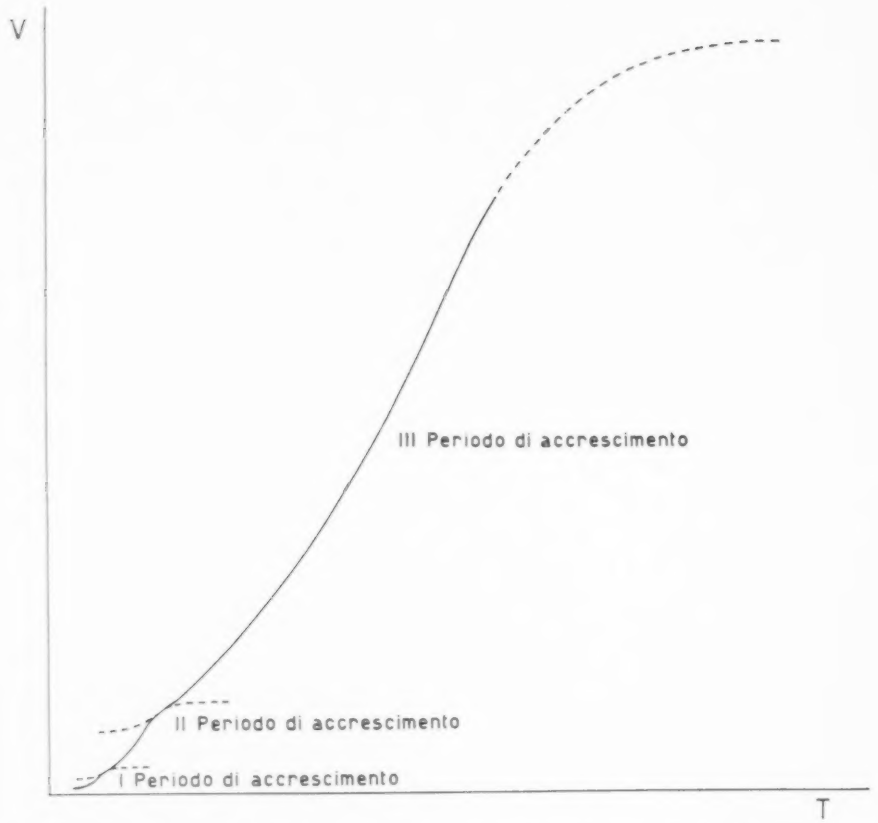

Diagramma 5. Curve ideali dei 3 periodi di accrescimento degli oociti. Le curve sono state costruite fissando i volumi massimi di ciascun periodo ed i tempi relativi e construendo le curve in base alle osservazioni (vedi il testo), ed ammettendo per ipotesi che si tratti di tre curve sigmoidi.

L'espressione più adeguata di questo processo, su cui si basa la maggior parte delle elaborazioni sull'argomento, è data dal rapporto nucleo-plasmatico. Questo rapporto è un indice della fisiologia cellulare in quanto esprime l'equilibrio morfologico dei componenti cellulari nelle diverse condizioni metaboliche ed ambientali delle cellule stesse. Le variazioni del rapporto nucleo-plasmatico in relazione allo stato fisiologico delle cellule possono essere espresse da una funzione iperbolica del diametro cellulare, con due costanti: i valori che può assumere la costante all'esponente (da 10^{-1} a 10^{-2}) indicano come il volume nucleare può essere proporzionale al volume cellulare, alla superficie cellulare ed al diametro cellulare ed esprime le diverse condizioni dello stato fisiologico delle cellule (Nozawa 1950).

Nelle cellule sia animali che vegetali in tessuti differenziati il valore del

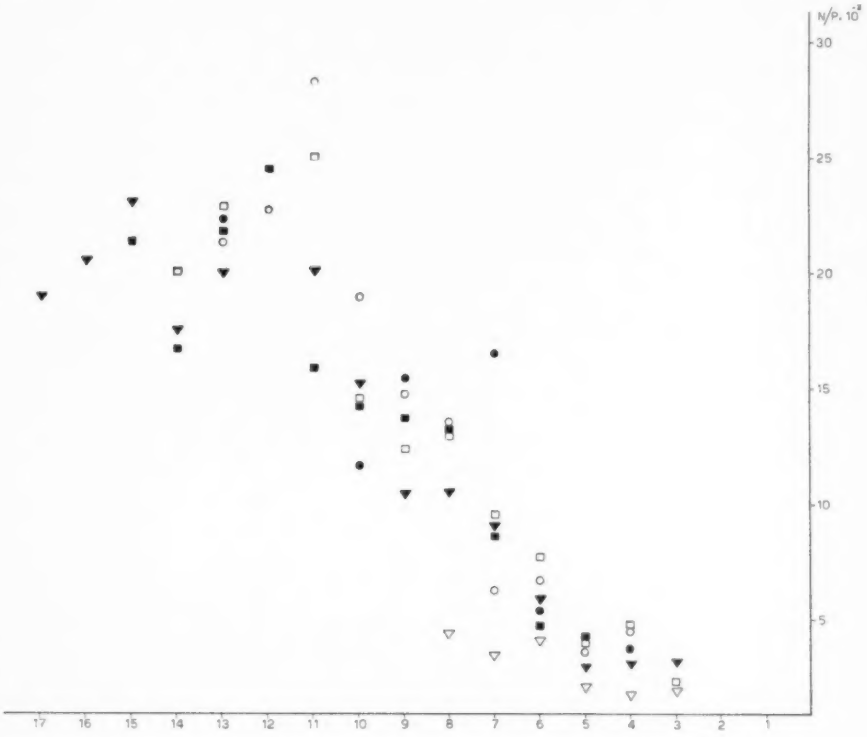

Diagramma 6. Andamento del rapporto nucleo-plasmatico nel 2° periodo di accrescimento. Sulle ascisse è indicata la successione degli oociti negli ovarioli (gli stessi dei diagrammi 2, 3 e 4), sulle ordinate il rapporto N/P espresso in valori moltiplicati per 10^{-2}. La maggior dispersione dei valori corrispondenti agli oociti da 10 a 17 è dovuta al fatto che le misure dei volumi del citoplasma sono soggette ad un errore maggiore per la forma irregolare delle cellule.

rapporto N/P ricavato con i tre metodi utilizzabili, citologico, chimico e spettrografico, è dell'ordine di 10^{-2} (Nozawa 1950).

Nella storia ontogenetica delle cellule e dell'organismo si hanno delle variazioni del rapporto nucleo-plasmatico che si scostano notevolmente da questo ordine di valori. Queste variazioni si riferiscono alle cellule in segmentazione (Godlewski (1918), Erdman (1909), Conklin (1912) ed altri), in queste il rapporto N/P in generale aumenta dall'ordine di 10^{-3} nelle uova non segmentate, al valore di 10^{-1} alla fine della segmentazione, quindi diminuisce a 10^{-2} nei tessuti differenziati (Nozawa). Questo comportamento è legato al particolare metabolismo delle cellule in segmentazione ed ai cambiamenti strutturali che si osservano nel nucleo e nel citoplasma in questo processo (cfr. Colombo 1950).

Anche queste variazioni non deviano dalle relazioni che regolano le dimen-

sioni dei componenti cellulari, e possono essere rappresentate dalla stessa funzione iperbolica con variabile il diametro cellulare (Nozawa).

Un interesse particolare hanno appunto gli oociti in accrescimento, i quali alla fine del processo di maturazione raggiongono un valore molto basso del rapporto nucleo-plasmatico, cioè dell'ordine di 10^{-3}.

Questo valore viene raggiunto dopo una serie di variazioni del rapporto che presenta degli andamenti diversi nelle varie fasi. Gli oogoni II e III presentano un rapporto N/P molto alto, nei preoociti si abbassa; aumenta leggermente nel leptotene e nello zigotene, non presentando degli scostamenti molto grandi. (Vedi tabella I e grafico I.) Nel secondo periodo di accrescimento il rapporto N/P diminuisce proporzionalmente all'aumento del volume degli oociti. (Diagramma 6.)

Dall'esame dei grafici si vede che in funzione del tempo (rappresentato indirettamente dalla successione degli ovociti nell'ovariolo) l'aumento del volume cellulare nel II periodo di accrescimento può essere espresso secondo una funzione iperbolica, infatti rappresentato graficamente, in valori logaritmici, dà approssimativamente una retta (diagramma 2); anche il rapporto nucleo-plasmatico diminuisce secondo una retta (diagramma 6) cioè in questo caso il volume nucleare aumenta in modo inversamente proporzionale al diametro cellulare. Teissier (1927) su oociti di *Hydractinia* in 2° periodo di accrescimento ha trovato che l'accrescimento del diametro nucleare è una funzione iperbolica del diametro cellulare ed ha calcolato empiricamente il valore dell'esponente; in osservazioni comparative (1930) ha visto che il comportamento citometrico di oociti sempre in tale periodo di accrescimento è uguale in diverse specie (di Celenterati) e la vitellogenesi si inizia a livelli diversi dell'accrescimento.

Queste particolari relazioni caratteristiche del 2° periodo di accrescimento indicano che il nucleo produce delle sostanze che si accumulano nel citoplasma. In *Anacridium* ed in generale negli Ortotteri, le relazioni volumetriche durante la vitellogenesi sono complicate dal fatto che per attività delle cellule follicolari si forma il tuorlo, il rapporto nucleo-plasmatico diminuisce ancora ed il volume nucleare, secondo le osservazioni del Matthey (1941), si riduce molto.

In quest'ultima fase dell'accrescimento oocitario le relazioni volumetriche tra nucleo e citoplasma probabilmente non rappresentano più delle relazioni funzionali, ma condizioni limite per le strutture cellulari che vengono spostate verso rapporti più equilibrati coll'attivazione dell'uovo e la segmentazione.

Da queste osservazioni si può concludere che anche le diverse fasi dello accrescimento oocitario presentano delle relazioni citometriche differenti che esprimono diversi stati funzionali del processo di differenziazione.

Ciò che risalta e merita di essere sottolineato tra i dati su riferiti, sono le condizioni citometriche degli oogoni II e III: essi presentano un rapporto

nucleo-plasmatico insolitamente alto, il volume nucleare è approssimativamente quasi la metà di quello della cellula tutta.

Questa condizione non è propria di cellule con alta attività moltiplicativa, ma io credo sia una caratteristica delle cellule germinali premeiotiche ed un indice della funzione autosintetica delle cellule germinali stesse per cui, in modo paradossale, si può che il germe sia rappresentato proprio dall'oogonio.

RIASSUNTO E CONCLUSIONI.

Sono state studiate le modificazioni morfologiche e particolarmente cariologiche e citometriche delle cellule germinali di ovari di *Anacridium aegyptium* (L.) dalla schiusa all'imagine, adoperando larve ed imagini schiuse ed allevate in laboratorio.

OL.
34
953

Le osservazioni sono state fatte su preparati per sezione (fissativi Dubosq-Brasil, Carnoy, Zenker formolico, Sanfelice) colorati con l'ematossilina ferrica, l'emallume-saffranina-orange, col metodo di Feulgen e col metodo di Unna-Pappenheim al verde di metile e pironina, e su preparati per schiacciamento in acido acetico 45% e colorati col metodo di Feulgen o con l'ematossilina ferrica. Sono state fatte anche osservazioni a fresco di ovarioli isolati.

1) *Modificazioni dell'ovario nel corso dello sviluppo larvale e nei primi periodi dello stato imaginale.* Alla schiusa l'ovario consta già di ovarioli, presenta una struttura simile all'ovario dell'imagine fin dalla 3ª muta. Nei primi stadi, e già subito dopo la schiusa, in ciascun ovariolo si trovano oogoni, preoociti ed oociti all'inizio della profase meiotica. Negli stadi larvali, dopo la 3ª muta, e nelle imagini, non molto dopo l'ultima muta, in ciascun ovariolo si trovano pochi oogoni, oociti in profase meiotica ed oociti in 2° periodo di accrescimento. Oociti in vitellogenesi si trovano soltanto parecchio tempo dopo l'ultima muta.

2) *Considerazioni sul ciclo oogenetico.* Dall'esame dell'ovario di larve in stadi diversi, di imagini che non avevano mai deposto e di altre dopo numerose deposizioni risulta che la scorta di oociti pronti per la vitellogenesi e per la deposizione non viene praticamente mai esaurita; il numero di ovarioli ed il numero di oociti non possono essere presi come indici di fecondità.

3) *La trasformazione degli oogoni in oociti.* Nei nidi di oogoni alcuni dei quali stanno per trasformarsi in oociti si trovano sempre zolle di sostanza basofila (A.R.N.), probabilmente formata da oogoni in degenerazione la quale forse interferisce nel processo di differenziazione.

Le modificazioni della struttura del nucleo nella differenziazione degli oogoni III in oociti preleptotenici può essere interpretata come cambiamenti strutturali della matrice cromosomica e variazioni degli avvolgimenti dei cromatidi.

4) *La struttura nucleare e cromosomica nella profase meiotica.* La struttura del nucleo negli stadi di preleptotene, di leptotene e di pachitene degli oociti è eguale a quella degli spermatociti negli stadi corrispondenti. Dopo il pachitene si osserva negli oociti un allungamento dei cromosomi, in fasi più avanzate del postpachitene (corrispondenti al pachitene ed al diplotene) i cromosomi perdono la Feulgen positività; nei preparati per sezioni non sono più chiaramente visibili, a fresco si riconoscono con la struttura a «lamp-brush». Se si esaminano nei loro passaggi graduali, le trasformazioni della struttura cromosomica nelle fasi suddette possono essere interpretate come svolgimenti di strutture elicoidali a livello microscopico. Nell'ultima telofase oogoniale i cromosomi, grossi e corti, presenterebbero tre avvolgimenti, l'uno compreso nell'altro (il «*minor*», il «*maior*» ed il «*super*» secondo lo schema di Cleveland), al preleptotene manca l'avvolgimento «*super*», al leptotene si svolge anche l'elicoide «*maior*» ed al pachitene i cromosomi presenterebbero solo l'avvolgimento «*minor*»; questo si svolgerebbe nel postpachitene colla formazione dei «*lamp-brush*» cromosomi.

5) *L'apparato siderofilo endonucleare.* Nei nuclei degli oociti in 2° periodo si sviluppa dai nucleoli un apparato formato da una fila di piccoli nucleoli riuniti da un filamento. Questo apparato può essere messo in evidenza soltano colla colorazione all'ematossilina ferrica, coi coloranti per l'A.R.N. si osserva soltanto reazione positiva diffusa. Questa formazione viene interpretata come due cromosomi eterocromatici che hanno probabilmente le funzioni di un apparato nucleolare nel corso del 2° periodo di accrescimento oocitario.

6) *L'accrescimento oocitario.* L'accrescimento volumetrico degli oociti viene diviso in 3 periodi: un primo periodo fino alla stadio di pachitene, un secondo periodo fino all'inizio della vitellogenesi, ed un terzo periodo caratterizzato dalla vitellogenesi vera e propria, cioè la formazione del tuorlo figurato. Questi tre periodi presentano delle caratteristiche proprie anche dal punto di vista citometrico: si tratta probabilmente di tre funzioni iperboliche diverse.

Il rapporto N/P passa da un valore superiore a 0,5 degli oogoni ad un valore inferiore a 10^{-3} alla fine dell'accrescimento oocitario. L'andamento delle variazioni del rapporto N/P durante il 2° periodo di accrescimento indica che in tale periodo l'accrescimento nucleare è proporzionale all'aumento del diametro cellulare.

CONCLUSIONS AND SUMMARY.

This paper provides an account of the morphological modifications and nuclear and cytometrical changes that take place during the development of

VOL. 34 195

the germinal cells in the ovary of *Anacridium aegyptium* L., as studied in laboratory reared larvae and adults.

The observations were carried out on material treated with different fixatives, (Dubosq—Brazil; Carnoy; Zerker-formol; and Sanfelice), sectioned, and then stained in either Iron Haematoxilin, Haemalum-Saffranin and Orange G.; Feulgen or Unna-Pappenheim methyl green and pyronine. Material was also squashed in 45 % acetic acid and then stained with Feulgen or Iron Haematoxylin. Surviving isolated ovarioles were also examined with phase-contrast.

1) *Modifications of the ovary during larval development and the first imaginal stages.*

After hatching the ovary consists of ovarioles and shows similar structure to those present in imagos at the end of the 3rd moult. In the first stages immediately after hatching in each ovariole there are oogonia, pre-oocytes and oocytes in the early prophase stages of meiosis. In the larval stage after the 3rd moult and in adult not long after the last moult in each ovary one finds a few oogonia, some oocytes in meiotic prophase and oocytes in their second stage of growth. Oocytes with yolk are only found some time after the last moult.

2) *The oogenetic cycle.*

From examinations of the ovaries of larvae of different stages and of adults that have not yet laid, together with others that have laid many times, it appears that the development of eggs ready for the reception of yolk deposition and for laying are never exhausted. The number of ovarioles and the number of oocytes can not be taken as an indication of the degree of fecundity.

3) *The transformation of the oogonia into oocytes.*

In a group of oogonia that are beginning to be turned into oocytes one always finds a mass of basophil substance (R.N.A.), formed from degenerating oogonia and which probably plays a role during the differentiation.

The modification of the structure of the nucleus in the differentiation of the tertiary oogonia in preleptotene oocytes can be interpreted as a change in structure of the chromosomal matrix and a variation in the coiling of the chromatids.

4) *The nuclear and chromosomal structure during meiotic prophase.*

The structure of the nucleus in the preleptotene, leptotene, and zygotene stage of the oocytes is similar and corresponds to the same stages of the spermatocytes.

After zygotene the chromosomes elongate and in the post-pachytene stages (corresponding to the pachytene and diplotene) the chromosomes loose their

Feulgen-positive nature and are less clearly visible in sections, though in fresh preparation one can recognise the lamp-brush structure.

If one examines this gradual changes, the transformation of the chromatic structure in the above mentioned phases can be interpreted as changes of the coils at the microscopic level. In the late telophase oogonia, the short and thickened chromosomes show three coils condensed one into the other (the *minor*, the *major* and the *super* coils of CLEVELAND). At preleptotene they lack the super coil, at leptotene also the major coil is loosing and at zygotene the chromosomes have only the minor coil. This is then followed in the post-pachytene stage by the "lamp-brush" structure.

5) *The siderophile endonuclear apparatus.*

In the nuclei of the oocytes of the 2nd stage, there develops from the nucleolus a series of small nucleoli joined together in a thread. This can only be seen after staining with Iron Haematoxilin and if it is stained for R.N.A. one only finds a diffuse positive reaction. This formation can be interpreted as due to heterochromatic chromosomes which probably function as a nucleolar apparatus during the 2nd period of growth of the oocyte.

6) *The growth of the oocyte.*

The increase of volume of the oocyte can be classified onto three periods: one ending at the pachytene stage, the second up to the deposition of yolk, and the third with the deposition of yolk. These three periods each show a characteristic cytometrical difference and thus probably have diverse functions.

The N/P ratio falls from a value of more than 10^{-1} in the oogonia to a value less than 10^{-2} at the end of oocytic growth. The change in the N/P ratio during the second period of growth indicates that in this period the growth of the nucleus is proportional to the increase in cell diameter.

(English title: Oogenesis in the Orthoptera. I. Histological and cytometrical analysis of oogenesis in *Anacridium aegyptium* (L.), from hatching to the adult.)

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VOL. 34 1953

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VOL. 34 1953

PATTERNS OF MATING BEHAVIOUR IN THE DOMESTIC BUFFALO

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CONTENTS.

Materials and Methods 234
Results 235
A. Female behaviour 235
B. Male behaviour 236
Discussion 236
Summary 238
Literature cited 238

In the course of mammalian evolution, patterns of sexual behaviour of increasing complexity have arisen, the main tendency of which is to secure an effective synchronisation of the essential reproductive conditions of the two sexes. Each species displays a characteristic pattern of sexual behaviour, considerable individual variations do exist. This variation is greatest among the infrahuman primates due to the great plasticity of behaviour in species at such phylogenetic level (YOUNG 1941). The restriction of mating to the oestrous phase of the female cycle provides economy of the male gametes and prevents exhaustion of the male. Mating as a social behaviour is a result of environmental, neural, physiological (including endocrinal factors), genetic and age factors.

The constancy of the surrounding environment (changing the pen, personnel or etc.) acts as a conditioned reflex to sexual behaviour in the two sexes as shown in the mare (LOWE 1938) and the ram (SOKOLOVA 1940). The excitatory value of a female is determined by exteroceptive factors such as colour and texture of the skin (HAFEZ 1951, 1952). In Rambouillet ewes, mating activity is higher with Hampshire rams than with Rambouillet rams (CHITTENDEN & WALKER 1936). In some species there is a tendency for mating to be initiated at some particular time of the day as observed in dairy cattle (WERNER *et. al.* 1938; TRIMBERGER 1948), sheep (QUINLAN *et al.* 1932; MCKENZIE & TERILL 1937) and rodents such as the gerbil, golden hamster, guinea pig, mouse and rat (reviewed by ASDELL, 1946).

Some components at least of the sexual behaviour, are short arc reflexes elicited independently of the higher centres, but the occurrence of which depend

strictly on hormonal conditions. BEACH (1947 a) has shown that patterns of sexual behaviour are partly controlled by hormones which affect metabolic processes involving many unrelated types of response. Oestrogens, progesterones (RING 1944; ASDELL *et. al.* 1945) and even androgens are implicated in the manifestation of oestrous behaviour. In cattle, oestrogen injections after ovariectomy have shown that intense oestrous behaviour may be evoked at very low hormone levels, thus indicating that oestrogens produce the psychical symptoms of heat (DE ALBA & ASDELL 1946).

In the male, erection and ejaculation although they both involve voluntary muscular contractions and cortical coordination are primarily innervated through the sacral autonomic nerves and may be caused to function independently of the motor copulatory pattern (WALTON 1950). Homosexual behaviour is recorded only in certain species (YOUNG 1941) and it may be induced by hormones (YOUNG & RUNDLETT 1939).

The buffalo is a member of the ox-tribe family, subfamily Bovinae. Out of five species in the wild condition, there is only the Asiatic buffalo (Bos (Bubalus) bubalis) which is now domesticated and is found in many tropical and subtropical countries (reviewed by HAFEZ 1952). The Asiatic buffalo has been divided into two races, a swamp race without a neck to the scrotum and with nocturnal mating (ASDELL 1946). The other, the river race, has a pendulous scrotum and with daytime mating (MC GREGOR 1941).

Mating behaviour has been given but little systematic study. Most workers have distinguished periods of receptivity and have not concerned themselves with the degree of these manifestations. Sexual behaviour during the four phases of the oestrous cycle (prooestrus, oestrus, metaoestrus & dioestrus) have been fully described in the domestic animals, mainly the cow (HAMMOND 1927; ROARK & HERMAN 1950), mare (ANDREWS & MCKENZIE 1941) and the ewe (MCKENZIE & TERRILL 1937). Physiological and physchological studies of sexual behaviour in mammals have been reviewed by BEACH (1947 b). The present study deals with the characteristics of mating patterns of the domestic buffalo in both sexes.

MATERIALS AND METHODS.

Twentyfour non-pregnant Egyptian buffalo-cows and four potent buffalo-bulls were kept at the Animal Breeding Research Farm, Cairo, Egypt. They aged from two to eight years and were fastened to double row stables by means of chains and neckhalters. Each buffalo-bull was joined with six buffalo-cows from two to four times daily in a paddock at regular intervals. Mating behaviour was studied in the two sexes over a period of six months from October 1951 to March 1952. Expectancy list was prepared for all females and a record was made for all females showing oestrous activity with parti-

VOL. 34 1953

cular attention to the time of day. The degree of receptivity in the buffalo-cows was determined by the reaction to the teaser and the sensitivity of the external genetalia to manual friction. Notations were made on the behaviour of females in and out of oestrus. The notations included such items as feeding habits, association with and attention to other animals in the same group, homosexual activity, frequency of urination and defecation and milk production. In addition to the periodic inspection, the herd attendants were instructed to report all peculiarities which might happen at night. Notations on the behaviour of the males were also made, the males being with or without aprons (on the bulls' bellies). The different males were tried with females of different ages and sizes. Behaviour during force mating (serving non-receptive females) was also noted. All animals under observation were fed with concentrates (crushed maize, bran & cottonseed cakes) and green fodder (green clover or maize).

RESULTS.

A. FEMALE BEHAVIOUR:

As active heat approached, the female tended to become restless. She roamed around the paddock and at other times stood quietly with her head held in the air. She twitched her tail frequently and often raised it. In the majority of cases the vulva of the receptive female was sniffed by other animals whilst the receptive female was never observed to sniff the external genitalia of other herd members. Changes in the eagerness to eat was noted and in a few cases the oestrous buffalo went off-feed. Changes in milk production was also noted, these were not reliable indication of oestrus because of tremendous individual variation. For the most part, only these animals showing intense psychical symptoms of oestrus were erratic in their feeding habits and in milk production. Urination was frequent during oestrus but there was no change in the frequency of defecation. In general the signs of oestrus were intensified by exercise and association with other animals especially males, as well as by stimulation of the vulva or clitoris by friction.

The onset of oestrous activity was from 6 P.M. to 6 A.M. in 84 % of the cases. It was often gradual, in 15 % of the cases it was abrupt; i.e. there was no prooestrus. The duration of the oestrous period varied from 10 to 43 hours. The cessation of oestrus was in most of the cases gradual, metaoestrus being quite distinguishable. During prooestrus and metaoestrus the females stood for the male, were receptive to him but did not allow mounting. During oestrus, females allowed mounting by the buffalo-bull with less certainity than in other species (cattle or sheep). They did not show any particular preference to a particular buffalo-bull. If the female was mounted by the male during the non-receptivety period (force mating) she would arch the back and run away. Homosexual behaviour (mount other females

or be mounted by others) amongst females was indistinguishable in the presence or absence of the male.

There were individual differences in sexual interest. Certain individuals manifested pre-mounting grunt during receptivity even in the absence of the buffalo-bull. This phenomenon seemed to be characteristic for the individuals since they repeated the grunt during the successive oestrous cycles, also their dams were reputed with the grunt. Some receptive females were persistent in being close to the buffalo-bull whilst others were attracted to the bull only when he made sexual approaches. Certain individuals, however, allow mating with great difficulty.

B. MALE BEHAVIOUR:

The buffalo-bull smelled receptive females, licked their external genitalia, raised his head and sniffed. Erection took place before mounting whilst protrustion, penetration and ejaculation came last. Before ejaculation, the glans penis hardened but without any great enlargement and vibrated rapidly giving much the same appearance as the urethral process of the mating ram. Fierceness was only observed at the time of ejaculation. The males did not show any offensive reaction towards the buffaloes after mating. The time interval between two successive copulations ranged from 30 seconds to 20 minutes according to sequence of service and the degree of receptivity of the female. After three consecutive services, the buffalo-bull showed exhaustion and efforts in mounting. Sometimes he explored genitalia and did not attempt to mount. At least, four hours of rest (apart from any female) had to elapse to revive sexual libido.

Sex drive exhibited by the bull was considerably variable according to size and age of the female. The different bulls showed preference to particular females. After copulating such females, the bull would refuse to serve any other female even if the latter was receptive. Certain buffalo-bulls showed greater sexual interest towards big-size females than to their age mates. When there was big-size difference between the two sexes, the male tended to ejaculate with less certainity to penetrate. After force-mating non-receptive females, the male was greatly attracted to them. When an apron was used to cover the whole belly and external genitalia of the male, his sexual libido did not decrease either during or after removing the apron. Heavy rainfalls and severe hot climatic conditions depressed the sexual desire whilst water sprinkling stimulated teasing action.

DISCUSSION.

The females exhibit several patterns during the receptivity period. It seems that the stimulus of these mating patterns is a combination of visual, auditory,

VOL.
34
1953

olfactory and tactile factors. It is possible that the normal metabolic processes in the animal is complicated by the conditions involved in such patterns. Frequent urination during receptivity is almost due to neural factors. The buffalo seems to be consistent with other species (cow, ewe & rodents) in showing a tendency for oestrus to begin more frequently during a particular time of the day. However the period of the day varies with the species. In cattle the majority of the oestrous cycles begin in the A.M. (Roark & Herman 1950) whilst in the buffalo it occurs frequently in the P.M.

In the male there are different degrees of sexual excitability as determined by the sexual value of the female. This sexual value does not seem to be correlated with the degree of her receptivity. Particular symphathy may be involved.

Some patterns in the behaviour of the males may be considered more or less as species-specifics. There is a considerable difference in the pattern of the bull (cattle) and the buffalo-bull, in the former the protrusion of the penis occurs before mounting whilst in the latter mounting occurs before protrusion and actual penetration. The preference of the male to particular females is a phenomenon often found among wild animals which are frequently monogamous. Meanwhile the females do not show any preference towards particular male. It seems likely that there are sex differences in the way that the animal respond to the mating stimuli. The genetic background of mating behaviour in relation to individual differences is of great academic interest.

The duration of the receptivity period varies considerably within the individuals. The duration of oestrus is dependent on the length time that the central nervous system responds to oestrogens as postulated by Asdell *et. al.* (1945). Prooestrus and metaoestrus could be easily confused since the psychical symptoms are so similar and the changes are gradual.

Various hormones exert specific effects on particular behaviour patterns in different ways. It is possible that in some cases the functions of critical sensory receptors are altered in the presence of essential hormones. Beach (1947 b) has shown that some types of the mating behaviour exhibit specific and intimate affiliation with hormones while others are independent of any additional form of hormonal control. There is probably a complicated cycle of processes in which the anterior pituitary (gland controlling sexual process), thyroid gland (regulating metabolic processes) and other endocrine organs play a part in the participation of mating behaviour in the two sexes. Whether the action of the hormones is directly upon the central integrating mechanism or whether it is indirect has not been definitely established, although it has been shown by Dempsy and Rioch (1939) that oestrous behaviour is expressed in the absence of afferent impulses from the genitalia.

SUMMARY.

Mating behaviour in both sexes of the Egyptian buffalo has been studied in relation to varying conditions. The stimulus of mating is a combination of visual, auditory, olfactory and tactile stimuli. Some patterns, however, are species-specifics. In the domestic buffalo *Bos (Bubalus) bubalis* L., there is no homosexual activity and mating tends to start in the P.M. or the early A.M. In the male, mounting occurs before protrusion whilst fierceness or offensive reaction are not observed. There are individual differences in both sexes in the degree of sexual excitability. Males show preference to particular females, this is not true for females. Sex differences in the way that the animal responds to mating stimuli is suggested. No literature on the heredity influence on sexual behaviour is available. Exteroceptive and hormonal factors involved in psychical symptoms of mating are reviewed and augmented.

VOL. 34 1953

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OL.
34
953

VOL
34
195

UNTERSUCHUNGEN DER KIEFERMUSKULATUR UND DEREN INNERVATION BEI SCHILDKRÖTEN

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Mit 11 Abbildungen. (Eingegangen am 23. 3. 1953.)

VOL. 34 953

INHALTSVERZEICHNIS.

Einleitung 241
Anatomischer Teil 243
I. Muskulatur 243
a) M. adductor mbd. externus 244
b) M. adductor mbd. posterior 256
c) M. adductor mbd. internus 258
d) M. intramandibularis 263
e) M. intermandibularis 264
II. Innervation 267
Vergleichender Teil 278
I. Muskeln 278
a) M. constrictor I dorsalis 278
b) M. adductor mbd. externus 279
c) M. adductor mbd. posterior 281
d) M. adductor mbd. internus 282
e) M. intramandibularis 283
f) M. intermandibularis 283
II. Nerven 284
Zusammenfassung 288
Synonyma 290
Abkürzungen 291
Literaturverzeichnis 291

EINLEITUNG.

An älteren Arbeiten über die Kiefermuskulatur der Schildkröten liegen nur wenige vor, in denen, von den ersten sorgfältigen Untersuchungen BOJANUS' abgesehen, nur allgemeine, Feststellungen, unter weitgehender Vernachlässigung der Innervation, getroffen wurden. Erst in den Arbeiten der letzten Jahrzehnte wurden diese Verhältnisse bei den Sauropsiden genauer untersucht, obwohl auch in diesen Arbeiten immer nur wenige Vertreter einzelner Familien behandelt wurden. Als Grundlage für alle ontogenetischen Fragen liegen uns nur die Ergebnisse der Untersuchungen EDGEWORTH's und FUCHS' vor.

RUGE lieferte 1896 die ersten genauen Mitteilungen über die ventrale Kiefermuskulatur und deren Innervationsverhältnisse bei einigen Reptilien. Er stellte auch das Einteilungssystem der Visceralmuskulatur auf, das in der Folge von LUTHER, LUBOSCH und LAKJER übernommen wurde.

LUTHER (1909—14) beschäftigte sich besonders, auf die Vorarbeiten VETTER's (1874—78) an Fischen zurückgreifend, mit den Fragen der Homologie der Kaumuskulatur innerhalb der *Anamnia*.

ADAMS (1919) behandelte die Kaumuskulatur auch bei *Chelydra*, beschrieb jedoch die grossen Muskelpartien ohne genauere Unterteilung, so dass eine detaillierte Analyse nicht gut möglich ist.

LAKJER (1926), der sich vor allem auf die Vorarbeiten LUTHER's stützte und auch dessen Einteilungsprinzip der Trigeminusmuskulatur übernahm, füllte mit seiner Arbeit die bis dahin bestehende Lücke in der Kenntnis der Homologieverhältnisse, innerhalb dieser Muskulatur zwischen *Amphibia* und *Mammalia* weitgehend aus. Er stellte durch Untersuchungen an fünf Cheloniern, die den Familien der *Testudinidae, Cheloniidae, Dermochelyidae* und *Trionychidae* angehören bereits die allgemeine, für die Ordnung charakteristische Ausbildung der Muskulatur und deren nervöse Versorgung fest.

FUCHS beschrieb 1931 an Schildkrötenembryonen (*Podocnemis expansa, Chelone imbricata, Chelone mydas*) Unterkiefer und Unterkiefernerven, nachdem bereits 1915 seine sehr ausführliche Arbeit „Über den Bau und die Entwicklungsgeschichte des Schädels der *Chelone imbricata*" erschienen war.

LUBOSCH beschäftigte sich in seinen Arbeiten (1933, 1938) mit dem Vergleich der visceralen Muskulatur von Amphibien und Sauropsiden, dabei auch auf die Ergebnisse LUTHER's, LAKJER's und RUGE's zurückgreifend.

Eine gründliche Bearbeitung der vom Nervus trigeminus versorgten Kiefermuskulatur der Schildkröten schien mir nach Studium der auf diesem Gebiet vorliegenden Arbeiten angebracht. Durch Untersuchungen an einer möglichst grossen Zahl von Familien wollte ich die bisherigen Ergebnisse der Autoren auf breiterer Basis, mit strengster Berücksichtigung der Innervation, überprüfen und erweitern. Vor allem fand ich Kontrolluntersuchungen der Resultate LAKJER's angezeigt, da durch die Bearbeitung seines Manuskriptes post mortem Lücken aufscheinen und sowohl LUTHER wie auch LUBOSCH und zuletzt HOFER und POGLAYEN zahlreiche Irrtümer nachweisen konnten. Auch beabsichtigte ich die Untersuchungsergebnisse von FUCHS (1931) zu ergänzen. Besonderen Wert legte ich auf die Art der Ausbildung des intermandibularen Muskels, den LAKJER nicht in seine Untersuchungen einbezog und dessen Innervationsverhältnisse auch in neuerer Zeit noch nicht völlig geklärt wurden. Untersuchungen von HOFER (1950) und FIEDLER (1951) ergaben bei Vögeln ein klares Nervenschema, das keine grundsätzlichen Abweichungen zeigte. Es sollte nun untersucht werden, ob ein so ausgeprägtes, starres Nervenschema auch bei Schildkröten vorhanden ist, oder ob hier auffallende Variabilitäten vorliegen.

Untersucht wurden:

Fam. *Dermochelyidae*	*Dermochelys coriacea* (*Sphargis* c.)
Fam. *Cheloniidae*	*Caretta caretta* (*Thalassochelys* c.) 2 Expl.
Fam. *Chelydridae*	*Chelydra serpentina* 2 Expl.
Fam. *Kinosternidae*	*Sternotherus odoratus* (*Cinosternum odoratum*)
„	*Kinosternon scorpioides*
„	*Kinosternon leucostomum*
Fam. *Testudinidae*	*Chrysemys picta*
„	*Pseudemys scripta troostii* 2 Expl.
„	*Malaclemys pileata littoralis*
„	*Graptemys pseudogeographica* (*Malaclemys lesueurii*)
„	*Terrapene triunguis* (T. *cinosternoides*)
„	*Cuora amboinensis* (*Cyclemys* a.) 3 Expl.
„	*Clemmys caspica*
„	*Clemmys guttata*
„	*Emys orbicularis* (E. *lutaria*, E. *europaea*) 2 Expl.
„	*Testudo graeca* (T. *ibera*) 2 Expl.

Fam. *Chelidae*	*Chelodina longicollis* 3 Expl.
„	*Batrachemys nasuta* (*Rhinemys* n.)
Fam. *Pelomedusidae*	*Pelusios niger* (*Sternothaerus niger*)
Fam. *Trionychidae*	*Amyda sinensis* (*Trionyx* s.)

Die von mir verwendete Nomenklatur und Einteilung der Kaumuskulatur entspricht dem von RUGE und LUTHER aufgestellten und von LAKJER und LUBOSCH übernommenen Einteilungsprinzip.

Für die Überlassung eines Arbeitsplatzes und reichen Untersuchungsmaterials möchte ich dem indessen verstorbenen Prof. Dr. OTTO STORCH, Vorstand des Zoologischen Institut der Universität Wien, ergebenst danken. Ich danke besonders Dozent Dr. HELMUT HOFER, der mich auf das Thema hinwies und mich bei meiner Arbeit beriet. Doz. Dr. KRAUSE und Dr. v. HOCHSTETTER vom Anatomischen Institut Wien, will ich für ihr grosszügiges Entgegenkommen durch Überlassen reichhaltigen Tiermaterials auf diese Weise meinen Dank aussprechen. Die Herren Dr. EISELT und Dr. h. c. KLEIN vom Naturhistorischen Museum in Wien, gestatteten mir freundlichst in die Schädelsammlung des Museums Einblick zu nehmen.

VOL.
34
953

ANATOMISCHER TEIL

I. MUSKULATUR.

Wir unterscheiden, im Bereich des Kieferbogens, Constrictor I dorsalis (nach FUCHS und EDGEWORTH bei Schildkröten nur als Embryonalanlage vorhanden), Adductor mandibulae und Constrictor I ventralis.

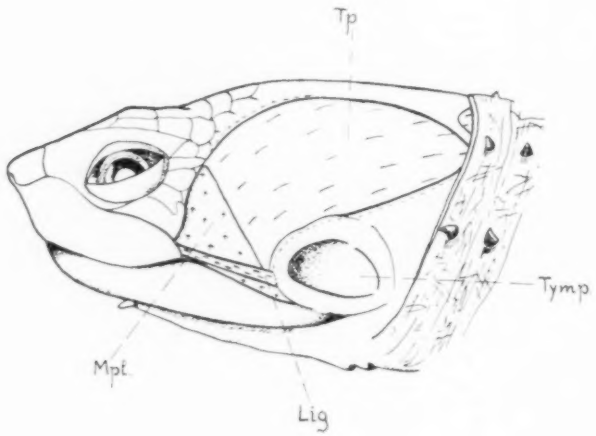
Die Terminologie geht auf die Muskulatur des Mandibularbogens bei den Selachiern zurück, bei denen man als primären Zustand drei Constrictoren vorfindet.

1. Constrictor I dorsalis ($M.C_1d$), der vom Schädel zum Palatoquadratum zieht und dessen primäre Aufgabe die Bewegung desselben gegenüber dem Neurocranium ist; seine Innervation erfolgt durch Nerven, die vom Ganglion trigemini direkt entspringen.
2. Lateraler Constrictor, der vom Palatoquadratum zur Mandibel zieht und die Mm. adductores mandibulae bildet, die ihre Nerven vom Stamme des Ramus tertius nervi trigemini erhalten.
3. Constrictor I ventralis, M. intermandibularis genannt, der die Unterkieferhälften ventral, bis zur Symphyse miteinander verbindet und sowohl die Unterkieferäste zusammenzieht als auch den Mundboden hebt. Funktionell ist er nicht so selbständig wie die anderen Teile des Constrictor I, da er mit einem vom Nervus facialis versorgten intermandibularen Muskel ($M.C_2v$) zusammenarbeitet. Der oral liegende Intermandubularismuskel erhält die ihn versorgenden Nervenäste vom im Unterkiefer laufenden $R.V_3$.

Die Muskulatur des 2. bzw. 3. Visceralbogens, die dem Innervationsbereich des N.VII und N.IX angehört, führt die Bezeichnung Constrictor II und Constrictor III (RUGE, LUTHER, LUBOSCH).

Der Adductor mandibulae setzt sich aus drei Muskelzügen (Add. mdb. externus, posterior und internus) zusammen, von denen der Adductor externus aus drei und der Adductor internus aus zwei Portionen besteht. Der Add. externus liegt lateral, der Add. posterior caudal und der Add. internus medial vom $R.V_3$. Meist zieht auch der $R.V_2$ lateral am Add. internus vorbei, doch gibt es Ausnahmefälle (*Pseudemys, Testudo*), bei denen der $R.V_2$ medial vom Muskel läuft.

a) M. adductor mdb. externus: Dieser Teil der Kaumuskulatur ist bei allen Schildkröten besonders kräftig ausgebildet und nimmt, sowohl bei den Meeresschildkröten mit geschlossenem Schädeldach, als auch bei anderen Extremtypen, bei denen überhaupt kein knöcherner Schläfenbogen mehr vorhanden ist, den grössten Teil der oberen und unteren Schläfengrube ein. Der gesamte Muskel wird von einer starken, bindegewebigen Fascie bedeckt. Diese „Temporalfascie" (nach LAKJER) dient in der Occipitalregion einem Teil der epaxonischen Muskulatur und auf der ungefähren Höhe des Dorsalrandes der Orbita bis zum Dorsalrand des Tympanon, also medial vom Schläfenbogen, sofern ein solcher vorhanden ist, zahlreichen Fasern der oberflächlichen Schicht des Add. externus als Ursprungsgebiet. Die Fascie befestigt sich grösstenteils an der knöchernen Umrahmung der Schläfengrube, also medial am Rostralabschnitt des Squamosum und Quadratum, am Caudalrand des Postfrontale und an der Dorsalkante des Parietale, liegt dem Muskel eng an, begleitet ihn horizontal nach rostral ziehend, biegt dann ziemlich steil nach ventral, um schliesslich in der überaus kräftige, bindegewebige Mundwinkelhaut, die eine Tasche mit äusserer und innerer straff bindegewebiger „Mundplatte" (LAKJER 1926) bildet, einzustrahlen. Bei Formen mit reduziertem Schläfenbogen ist die Fascie einheitlich. Ob sie bei Formen mit erhaltenem Temporalbogen zweiteilig ist (LAKJER 1926, P. 48 f.), d.h. medial am Schläfenbogen mit dem oberen



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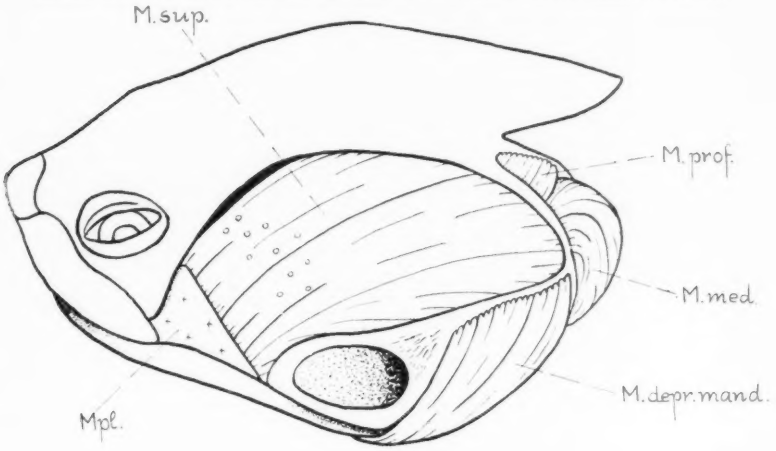
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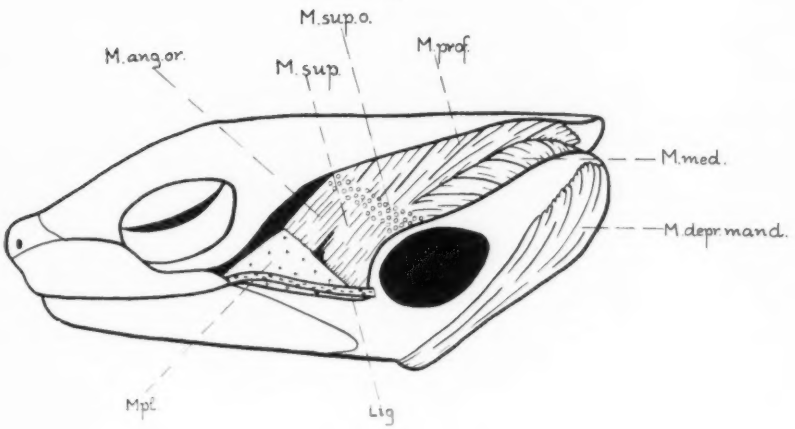
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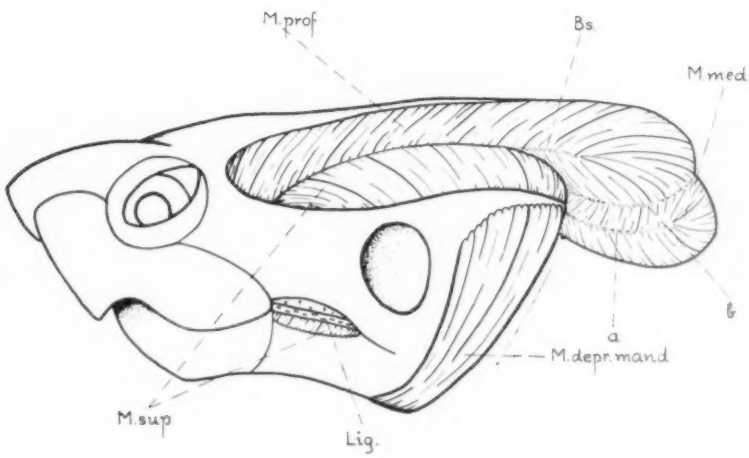
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D

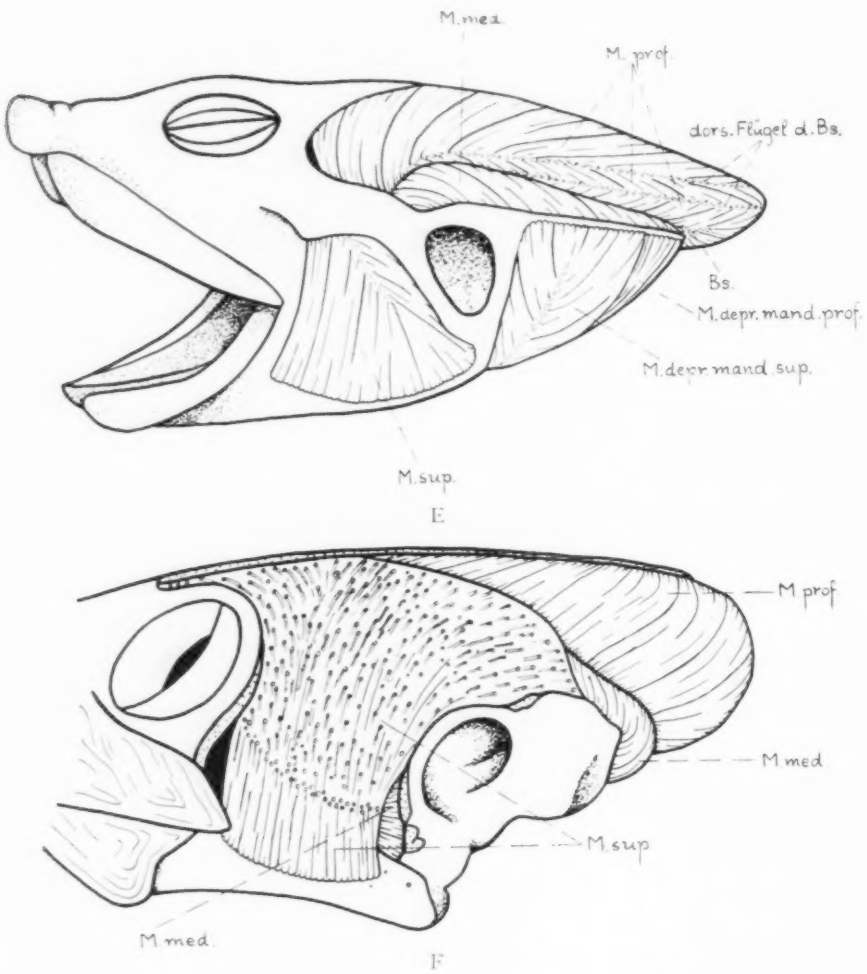


Abb. 1. Oberflächenansicht der Kiefermuskulatur.

A *Batrachemys nasuta*. Temporalfascie nach Entfernung der Haut; kein Schläfenbogen. B *Batrachemys nasuta* nach Entfernung der Temporalfascie. Darstellung der 3 Adductor externus-Schichten. C *Chelodina longicollis*. Dasselbe. Beachte M. anguli oris und streifenförmiges Ursprungsfeld der Portio superficialis an der Medialfläche der Temporalfascie. Kein Schläfenbogen entwickelt. D *Kinosternon scorpioides*. Oberflächenbild bei vorhandenem Schläfenbogen. E *Amyda sinensis*. Dasselbe. Beachte atypisches Verhalten der Portio superfacialis. F *Caretta caretta*. Oberflächenbild des Adductor externus nach Resektion des Temporaldaches.

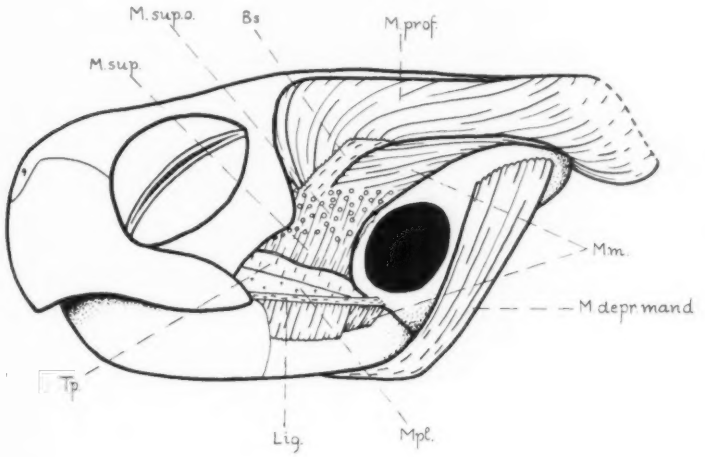
Teil ansetzend und mit dem unteren Teil entspringend, konnte ich nicht mit Sicherheit feststellen. Als ventralen Abschluss der Schläfengrube, in Ermanglung eines knöchernen Schutzes, wahrscheinlich auch um ein Einreissen der Mundwinkelhaut zu verhindern, finden wir bei den Schildkröten ein straffes

VOL. 34 1953

Ligament, das lateral der „Mundplatte" gelegen, Maxillare mit Quadratum verbindet. Häufig ist dieses Ligamentum quadrato-maxillare mit der „Mundplatte" bindegewebig verwachsen.

Der Adductor externus schliesst eine sehr kräftige, lange und breite Sehne in sich ein (LAKJER's „Bodenaponeurose"), die nur bei *Dermochelys* in Reduktion begriffen ist; sie dient der Hauptmasse der Fasern der drei Externuspartien zum Ansatz. Diese Sehne („Binnensehne"), zieht, in der oberen Schläfengrube caudo-dorsal vom Squamosum beginnend, mit mehr oder weniger dorso-ventral gehaltenen Flächen in rostraler Richtung. Im vorderen Teil der oberen Schläfengrube biegt die Sehne, dem Prooticum, an dessen Kante sie bei den Kaubewegungen gleitet, anliegend, nach ventral in die untere Schläfengrube, dabei ihre Flächen oft bis zu 90° in sagittale Richtung drehend und inseriert dorsal am Coronoid (Complementare nach FUCHS 1931) und zusätzlich auch am Dentale (*Chelydra*), am Dentale und Supraangulare (*Caretta*), oder auch an der Gaumenhaut medial vom Coronoid (*Chelodina, Batrachemys*). Die Binnensehne kann reiche Differenzierungen aufweisen, wie Taschenbildung (*Caretta, Cuora, Pelusios*), kammartige Fortsätze (*Caretta, Chelodina*) und caudale Abzweigungen in Form einzelner Sehnenfahnen (*Amyda, Kinosternon, Sternotherus*). Eine Besonderheit in der Ausbildung der Ansätze der Externusportionen ist bei *Terrapene* dadurch gegeben, dass nicht die ganze Oberfläche der Binnensehne den Externusfasern zur Insertion dient, sondern ein gewisses Gebiet, dorsal des Ursprungs der Superficialisschicht an der „Temporalfascie", nach Abtragung der Haut, freiliegt. Bei *Malaclemys* erstreckt sich das freiliegende Sehnenfeld weit nach caudal.

Die Unterteilung des Adductor externus in drei Portionen (Portio superficialis, P. media, P. profunda) ist fast immer deutlich; nur selten kommt es zu



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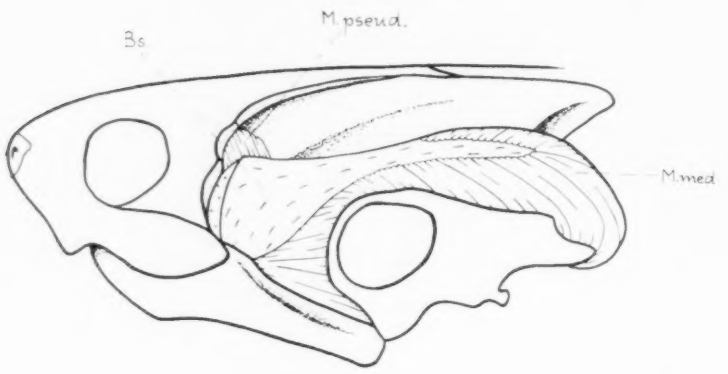

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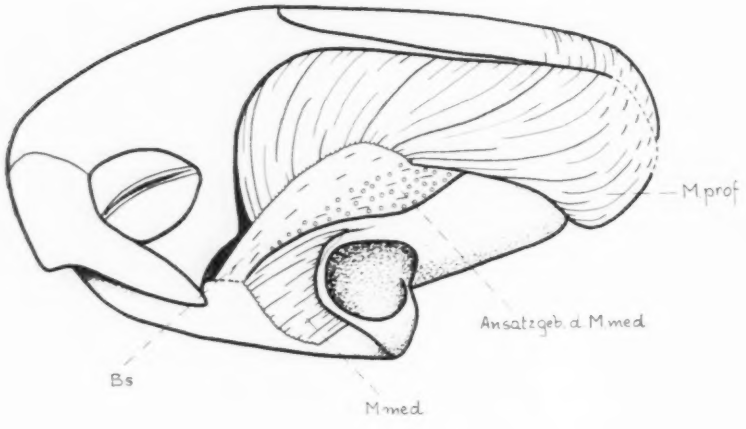

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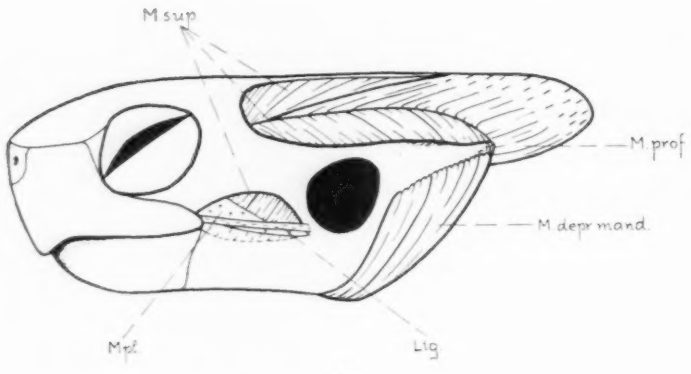

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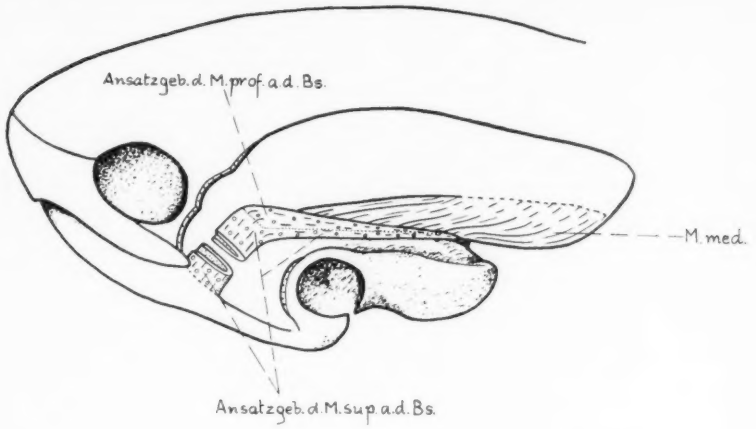
VOL. 34 1953



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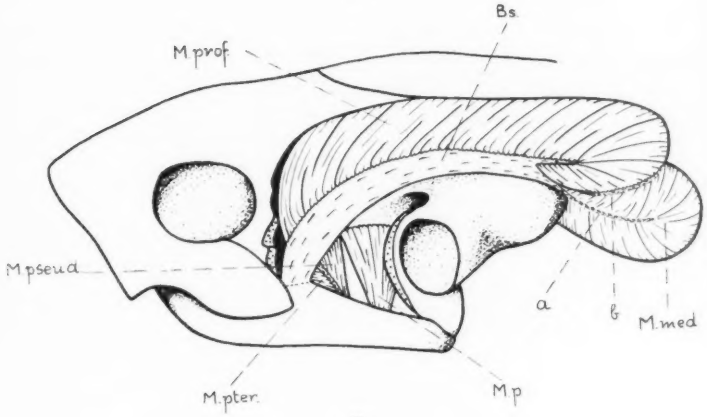

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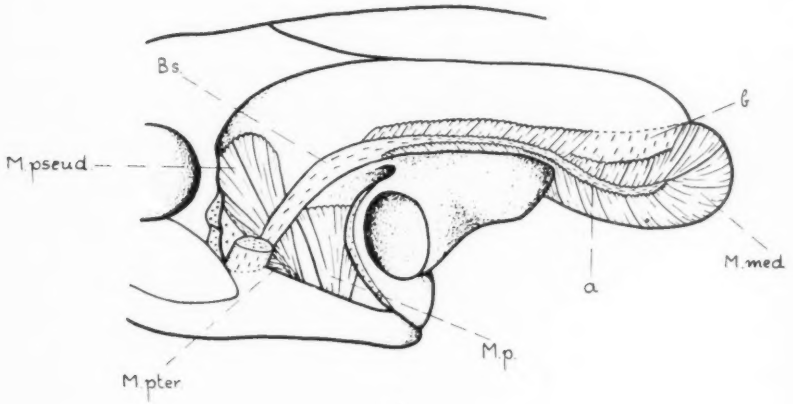

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Abb. 2. Schichten des M. adductor mand. externus.

A *Terrapene triunguis*. Oberflächenbild. B *Pelusios niger*. Darstellung der Portio media. C *Terrapene triunguis*. Darstellung der Portio profunda. D *Cuora amboinensis*. Oberflächenbild. Atypisches Verhalten der Portio superficialis. E *Cuora amboinensis*. Atypisches Verhalten der durch die P. superficialis in die Tiefe verdrängten P. media. F *Kinosternon scorpioides*. Muskelbild nach Abtragung der P. superficialis. G *Kinosternon scorpioides*. Atypisches Verhalten der P. media.

Übergängen zwischen einzelnen Portionen. Bei *Chelodina* ist keine deutliche Trennung der P. superficialis von der P. media und profunda wahrzunehmen. Bei *Batrachemys* finden wir einen Übergang zwischen P. superficialis und profunda in deren rostralen Abschnitten. Von selbständigen, isolierbaren Muskeln kann jedoch in keinem Fall gesprochen werden, weshalb ich auch die Bezeichnung Portionen einführte. Die allgemeinen Lageverhältnisse der 3 Portionen sind folgende: Die P. superficialis füllt in einer Sagittalebene den Grossteil der unteren Schläfengrube aus. Sie entspringt medial des Os jugale und Os quadratojugale. Die P. media schliesst medio-caudal an die P. superficialis an und entspringt oft mit den dorso-caudalen Fasern an der äusseren knöchernen Umrahmung der oberen Schläfengrube, wodurch sie auch dorsal ersterwähnter Portion zu liegen kommt. Die P. profunda schliesslich liegt medial beider Portionen und entspringt an der inneren knöchernen Umrahmung der oberen Temporalgrube, so dass auch diese Portion die P. superficialis dorsal überragt. In ihrem hinteren Ursprungsgebiet bildet die P. profunda einen Muskelballen, der meist caudal über den Occipitalkamm hinausreicht.

Die Versorgung des Adductor externus erfolgt durch meist zwei, lateral vom R.V_3 in dessen oberen Drittel entspringende, kräftige Nervenäste, welche niemals mit den den Add. internus innervierenden Ästen in Beziehung stehen.

Die oberflächlichste Portion des Add. externus — P. superficialis — beschränkt sich in der Regel auf das laterale Gebiet der unteren Schläfengrube; nur bei *Kinosternon, Sternotherus* und *Cuora* reicht der Ursprung bis weit in die obere Schläfengrube. Die Portion füllt die untere Schläfengrube nahezu in ihrer ganzen Breite aus und lässt nur in deren caudalstem Teil Fasern der P. media durchblicken, mit Ausnahme von *Chelydra, Kinosternon, Sternotherus* und *Amyda*, bei denen die P. superficialis so ausgebildet ist, dass keine Mediusfasern vor Abtragung der Superficialisschicht im ventrolateralen Abschnitt der unteren Schläfengrube sichtbar sind. Die P. superficialis besitzt mehrere Ursprungsgebiete, und zwar entspringen zahlreiche ihrer Fasern an der Medio-Rostralfläche des Quadratum, die Masse der Fasern jedoch an der „Temporalfascie" medial des Quadratojugale (Squamosum nach Lakjer) und Jugale, oder, bei Fehlen dieses Bogens, an der „Temporalfascie" entlang eines Streifens auf ungefährer Höhe des Dorsalrandes von Tympanon und Orbita. Bei *Chelodina* ist der Temporalbogen vollständig reduziert, bei *Terrapene* ist nur ein kleiner Rest des Quadratojugale erhalten. Oft kommt als zusätzliches Ursprungsgebiet für die rostralen Fasern die Caudo-Medialfläche des Postfrontale hinzu, wie bei *Clemmys, Emys, Malaclemys, Pseudemys, Caretta* und *Chelydra*, manchmal tritt auch der Dorso-Medialrand des Squamosum hinzu, so bei *Cuora* und *Kinosternon*. Die Fasern ziehen steil rostroventrad. Die äusseren Fasern setzen fleischig — *Caretta, Kinosternon, Clemmys, Testudo, Batrachemys* — oder leicht sehnig — *Dermochelys, Chelydra* — an der Dorso-Lateralfläche der Mandibel an. Mit der Lage der Deckknochen der

VOL. 34 1953

Mandibel variiert auch der Ansatz dieser Superficialisfasern. So liegt der Ansatz bei *Chelydra, Kinosternon, Testudo* und *Amyda* am Supraangulare und Dentale, bei *Dermochelys, Emys,* und *Batrachemys* am Supraangulare, bei *Clemmys* am Dentale und bei *Caretta* am Supraangulare und Coronoid. Bei *Malaclemys* greift der Ansatz der oberflächlichen Fasern weit nach ventral in eine breite Bucht des Dentale. Zuweilen strahlt der rostrale Teil der oberflächlichen Superficialisfasern in den Bug der „Mundplatte" ein (*Terrapene, Chelodina*); bei *Pelusios* setzen sämtliche oberflächliche Fasern an der „Mundplatte" an. Diese Befunde zeigen bei Schildkröten eine Parallele zum M. levator anguli oris der Sauria.

Die Masse der tieferen Fasern inseriert an der Rostro-Lateralfläche der mächtig ausgebildeten Binnensehne. Nur bei *Pelusios* setzen sie nicht an der Sehne, sondern am Dorsalrand des Coronoid an. Bei *Caretta* setzen die Fasern an der Lateralfläche der Binnensehne und ausserdem noch an einem kräftigen, niedrigen, von der Lateralfläche abgehenden Kamm doppelfiedrig an. Die Portio superficialis findet sich bei *Caretta, Cuora* und *Kinosternon* in besonderer Ausbreitung und Stärke vor. Das Ursprungsgebiet erstreckt sich bei *Caretta* auch auf den Rostralteil des Squamosum, der Ursprung vom Postfrontale wurde schon erwähnt. Bei *Chelydra, Malaclemys* und *Cuora* kommt noch ein Teil des Parietale hinzu, bei ersterer auch das Squamosum. Während bei *Chelydra* und *Malaclemys* nur wenige Fasern an der rostralsten Kante des Parietale entspringen, nehmen bei *Cuora* zahlreiche Fasern ihren Ursprung am rostralen Teil der Lateralfläche des Parietale und Squamosum, wodurch bei diesem Exemplar der Muskel eine auffallende Mächtigkeit erlangt. *Sternotherus* weist, im Gegensatz zu *Kinosternon,* eine recht schwache Portion auf, die nur am Quadratum und hintersten Teil des Quadratojugale entspringt. Als Einzelfall entspringen bei *Terrapene* die vom Quadratum kommenden Fasern sehnig. Eine Sonderstellung nimmt *Batrachemys* ein. Durch besonders starke Reduktion von unten her ist nur eine zarte, Parietale und Squamosum verbindende Spange als Rest des ehemaligen Schläfendaches übergeblieben. Die P. superficialis hat nun ihren Ursprung nach caudal bis an die „posttemporale Spange" (nach Zdansky 1924) verlegt. Sie bedeckt auf diese Weise laterodorsal die ganze Temporalgrube. Der Ursprung des Muskels liegt nun an der Medialfläche der „posttemporalen Spange", die ihrer Entstehung nach nicht der posttemporalen Spange der Lacertilier und *Hatteria* entspricht, am Quadratum, am obersten, hinteren Rand des Parietale und für einige Fasern ventro-rostral an der „Temporalfascie". Der Ansatz der Fasern liegt hauptsächlich an der Dorsalfläche der Binnensehne. Einige ventro-caudale Fasern inserieren, wie weiter oben erwähnt, dorsal am Supraangulare. Ebenfalls vom Allgemeintypus stark abweichend ist die Ausbildung der P. superficialis bei *Amyda.* Diese sehr breite, aber nicht kräftige Portion entspringt an der „Temporalfascie" medial vom Jugale und Quadratojugale. Der Muskel umschliesst

eine Sehne, deren Rostral- und Caudalfläche zahlreichen Fasern zum Ursprung dient. Diese Sehne ist nicht mit der Binnensehne identisch, sondern eine eigene Differenzierung der P. superficialis. Die vorderen Muskelfasern laufen leicht rostrad, die hinteren leicht caudad und inserieren sehr weit ventral, lateral am Dentale und Supraangulare.

Die mittlere Partie des Adductor externus — P. m e d i a — verhält sich in ihrer Stärke umgekehrt zu der der P. superficialis. So ist sie besonders kräftig bei *Pelusios, Pseudemys, Chrysemys* und *Dermochelys* und schwach bei *Cuora* und *Caretta*. In der Wahl ihrer Ursprungs- bzw. Ansatzgebiete verhält sie sich recht variabel. Der Muskel entspricht in der Regel medio-dorsal am Squamosum — bei *Batrachemys* an dessen Caudalfläche — und am Quadratum medial der P. superficialis. Als zusätzliches Ursprungsgebiet kommt bei *Emys, Chelodina, Pelusios* und *Amyda* die Dorsalfläche des Opisthoticum, bei *Caretta, Dermochelys* und *Terrapene* die Medialfläche des Quadratojugale hinzu. Die Muskelfasern ziehen bei *Chelodina, Kinosternon, Batrachemys* und *Pelusios* einen Ballen bildend, der bei letzterer die P. profunda caudal noch überragt, erst nach dorsal und biegen dann nach rostroventral um. Die dorso-caudal entspringenden Fasern inserieren lateral oder medial an der Binnensehne, die ventral abgehenden Fasern setzen an der Mandibel, medio-caudal der P. superficialis, an; nähere Angaben über das Ansatzgebiet dieser Portion werden wegen der grossen Verschiedenheiten für jedes Tier gesondert gebracht. Die Portion setzt bei *Dermochelys* lateral am horizontalen Teil der Binnensehne, am Grossteil der Rostro-Lateralfläche der Sehne in ihrem vorderen Verlauf und caudo-medial am Supraangulare, bei *Caretta* am Bug der Binnensehne, lateral und medial in ihrem oberen Abschnitt und sehnig medio-rostral am Supraangulare an. Bei *Pseudemys* und *Chrysemys* setzen die vom Squamosum kommenden Fasern am Caudalabschnitt der Lateralfläche der Binnensehne, die vom Quadratum kommenden Fasern am Dentale und Supraangulare an. Die Insertion liegt bei *Malaclemys* am Caudo-Ventralteil der Lateralfläche der Binnensehne und lateral am Dentale und Supraangulare; bei *Clemmys* liegt sie an der Lateralfläche der Binnensehne und an der Lateralfläche des Supraangulare. Bei *Emys* inseriert der Hauptteil der Fasern an der Medialfläche der Binnensehne in ihrem rostralen Bereich, nur wenige Fasern setzen lateral an ihren Horizontalflächen an. Bei *Terrapene* setzen die dorsalen, hinteren Fasern an der Lateralfläche der Sehne, die ventralen, vorderen Fasern an der Mandibel an. Der Ansatz der Fasern befindet sich bei *Testudo* an der Lateralfläche der Binnensehne. Bei *Pelusios* befindet sich die Insertion an der Ventralfläche und an den Rändern der Binnensehne. Die Binnensehne bildet bei diesem Tier in ihrem Ansatzbereich eine Tasche, die nach rostro-lateral offen ist, in der aber keine Muskelfasern ansetzen. Bei *Amyda* setzen die Fasern am Ventralteil der Latero-Dorsalfläche der Binnensehne und am Coronoid und Supraangulare an. Bei *Chelydra* entspringt die Portio media sowohl am Qua-

VOL. 34 1953

dratum, Squamosum und Opisthoticum, als auch mit ihren caudalsten Fasern, an einer Sehne, die den Muskelbauch der P. profunda ventral umgibt. Das Ansatzgebiet des Muskels befindet sich an der Caudo-Lateralfläche der Binnensehne und, caudo-medial von dieser, an der Mandibel. Bei *Kinosternon* und *Sternotherus* wird dieser Muskel durch die mächtig ausgebildeten beiden anderen Externusportionen weit nach caudal verdrängt, wo er, wie bereits erwähnt, einen Muskelballen bildet, der, ventral von dem der P. profunda gelegen, caudal über den Occipitalkamm hinausreicht. Der Muskel umschliesst den grössten Teil der Sehne a, die eine mediale Abspaltung der Binnensehne darstellt und durch ihren horizontalen Verlauf die P. media in eine dorsale und ventrale Partie zerlegt. Der Ursprung der dorsalen Fasern liegt an der Ventralfläche der Sehne b (diese Sehne ist aus den caudo-dorsalen Fasern der P. media entstanden), am Supraoccipitale und Parietale, ventral der P. profunda. Der Ursprung der ventralen Fasern befindet sich genau ventral der dorsalen Fasern, am Supraoccipitale und Parietale und an einer Sehne, die den Muskelbauch medio-ventral umgibt. Alle Fasern setzen an der Ventral- und Dorsalfläche der Sehne a an. Die bei *Cuora* besonders schwach ausgebildete Portion liegt ventral der P. profunda. Sie entspringt, in ihrem caudalen Abschnitt leicht sehnig, am Supraoccipitale und mit einigen Fasern auch am Opisthoticum. Ihr Ansatzgebiet liegt im Inneren der Tasche der Binnensehne, die nach medial offen ist und deren Bug nach lateral weist. Das Ursprungsgebiet der P. media bei *Chelodina* entspricht dem im Allgemeinschema dargestellten. Die Portion bildet caudal einen schwächeren Muskelballen, dessen medialer Teil von den caudo-lateralen Fasern der P. profunda überdeckt wird. Der Muskel inseriert an der Ventralfläche der Binnensehne und an dem caudo-medial von dieser abgehenden, kammartigen Fortsatz. Seine caudo-ventralsten Fasern setzen an der Dorso-Medialfläche des Supraangulare an. Bei *Batrachemys* nimmt diese Portion, unter Bildung eines kräftigen Muskelbauches, ihren Ursprung an der Caudalfläche des Squamosum und an der Dorsalfläche des Opisthoticum, ferner an der Dorsalfläche des Prooticum und endlich medial am Quadratum. Ihre Fasern inserieren an der Ventralfläche der Binnensehne.

Die Portio p r o f u n d a, die durchwegs die stärkste Portion des Adductor externus darstellt (Ausnahme *Dermochelys*) ist durch ihre Lage medial der Binnensehne gegen die beiden anderen Portionen besonders deutlich abgegrenzt. Sie reicht caudal meist über die P. media (Ausnahmen: *Kinosternon, Sternotherus, Chelodina*) und oft auch über das Hinterende des Supraoccipitale hinaus (*Dermochelys, Caretta, Chelydra, Terrapene, Pseudemys, Malaclemys*), weist einen mässig starken Muskelballen bei *Kinosternon, Sternotherus, Chrysemys, Clemmys, Testudo, Pelusios* auf und tritt nur bei *Emys, Chelodina, Batrachemys* und *Cuora* ohne Ballenbildung auf. Die Fasern nehmen ihren Ursprung an der Lateralfläche und Dorsalkante des Parietale und Supra-

occipitale, bei *Dermochelys* nur am Supraoccipitale, bei *Caretta* am Parietale, Supraoccipitale und am Bolen der oberen Schläfengrube. Sie ziehen rostro-ventrad und inserieren am Caudalende der Binnensehne, welches sie umgreifen und an der Medialfläche der Sehne bei *Chelydra, Pseudemys, Chrysemys, Clemmys* und *Emys*, ausserdem noch am freien Teil der Lateralfläche der Binnensehne bei *Testudo* und *Malaclemys*. Ferner inserieren die Fasern dieser Portion bei *Dermochelys* an der Dorsalfläche der Binnensehne in deren hinterem Verlauf und an der Rostralfläche in ihrem vorderen Verlauf. Bei *Caretta* erfolgt die Insertion in der Tasche der Binnensehne und an der der Schädelkapsel zugewandten Fläche ihres Innenflügels. Bei *Batrachemys* bedeckt die P. profunda mit ihren caudo-lateralen Fasern die P. media und inseriert, gemeinsam mit Fasern der P. superficialis, an der Dorsalfläche der Binnensehne. Bei *Pelusios* überdecken die caudo-medialen Fasern die P. media, der Ansatz liegt an der Dorsalfläche der Binnensehne. Bei *Kinosternon* und *Sternotherus* entspringt der Muskel am Parietale und Supraoccipitale, dorsal der P. media und an der horizontal liegenden Sehne b (siehe Beschreibung der P. media). Die rostral vom Hinterende der P. superficialis gelegenen Fasern der P. profunda inserieren an der Medialfläche der Binnensehne, die caudal vom Hinterende der P. superficialis gelegenen Fasern umschliessen das Hinterende der Binnensehne und inserieren somit an deren Dorsal- und Ventralfläche. Bei *Terrapene* liegt der Ursprung des Muskels am Parietale und Supraoccipitale, für einige Fasern auch am Postfrontale. Caudo-dorsal besitzt der Muskel mit der P. profunda der anderen Schädelseite einen gemeinsamen sehnigen Ursprung und zwar derart, dass die oberflächliche Faserschicht der P. profunda, im Bereich caudal des Supraoccipitale, in der Mediane in eine sehnige Raphe ausläuft, die am Caudo-Dorsalende des Supraoccipitale ansetzt. Die Insertion des Muskels erfolgt an der Medialfläche und am dorsalen Teil der Lateralfläche der Binnensehne. Der relativ schwache Muskel entspringt bei *Chelodina* am Supraoccipitale und Parietale. Nicht ganz so weit nach caudal reichend wie die P. media, bedeckt er deren medialen Teil. Die Portion setzt an der Gaumenhaut medial der „Mundplatte" und an der Dorsalfläche der teilweise in die Gaumenhaut einstrahlenden Binnensehne an. Bei *Amyda* entspringt die kräftige Portion an der Ventralfläche des Postfrontale, am Parietale und Supraoccipitale. Der Muskel umfasst das Caudalende der Binnensehne, deren Flächen nach ventro-medial und dorso-lateral weisen. Im caudalen Abschnitt ihrer Dorso-Lateralfläche hat die Sehne zwei auf ihr senkrecht stehende Flügel ausgebildet. Der Muskel setzt an der gesamten Medio-Ventralfläche der Binnensehne, am caudalen Abschnitt ihrer Dorso-Lateralfläche, an ihren beiden Sehnenflügeln, ferner im medialen Bereich der Dorso-Lateralfläche der Sehne in ihrem rostralen Abschnitt und schliesslich, mit einigen der rostralsten Fasern, am Coronoid und Dentale an. Der genaue Verlauf der Fasern zwischen den Sehnenflügeln ist aus der Abbildung ersichtlich.

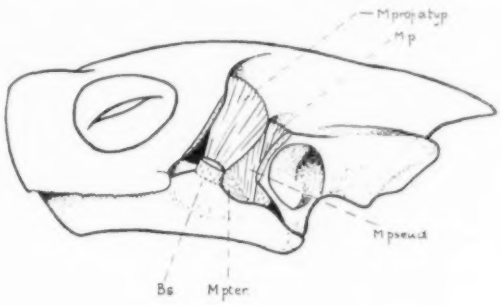
VOL. 34 1953

Bei *Clemmys* tritt der Muskel in zwei Portionen auf.

a) latero-caudale Portion (P.prof.typica): diese weitaus grössere Portion entspringt mit mässig starker Ballenbildung am Supraoccipitale und Parietale, umfasst das Caudalende der Binnensehne und inseriert ausserdem an deren Medialfläche. Sie weicht somit nicht vom Allgemeintypus der Profunduspor-tion ab.

b) medio-rostrale Portion (P.prof.atypica): bedeckt lateral die P. pseudo-temporalis des Add. internus, entspringt am ventro-rostralsten Abschnitt des Parietale, genau dorsal der P. pseudotemporalis und strahlt in den ventralsten Teil der Medialfläche der Binnensehne, kurz vor deren Ansatz, ein. Diese Abspaltung der grossen caudo-lateralen Portion findet sich bei *Clemmys caspica*, nicht aber bei *Clemmys guttata* (andere *Clemmys*-arten wurden noch nicht untersucht) vor.

Bei *Cuora* liegt die P. profunda dorsal der P. media und entspringt, ohne Ballenbildung, mit ihren dorsalen Fasern sehnig, am Supraoccipitale und Parietale. Ihr Ansatz befindet sich am Medialteil der Horizontalfläche der Binnen-



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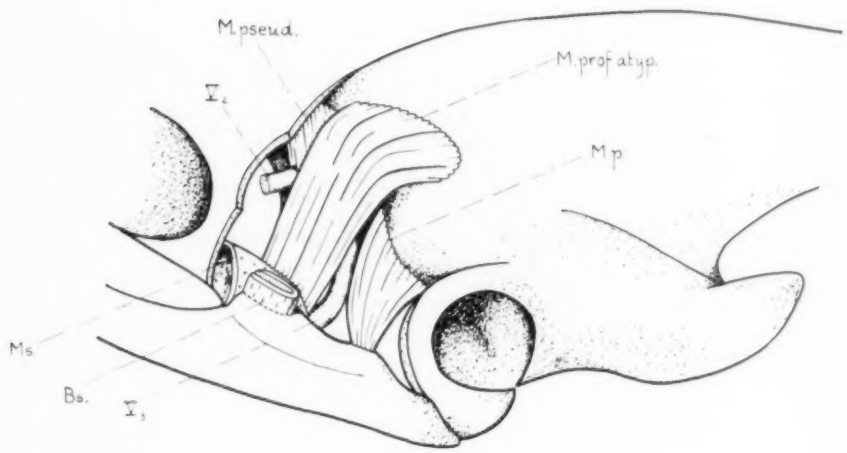

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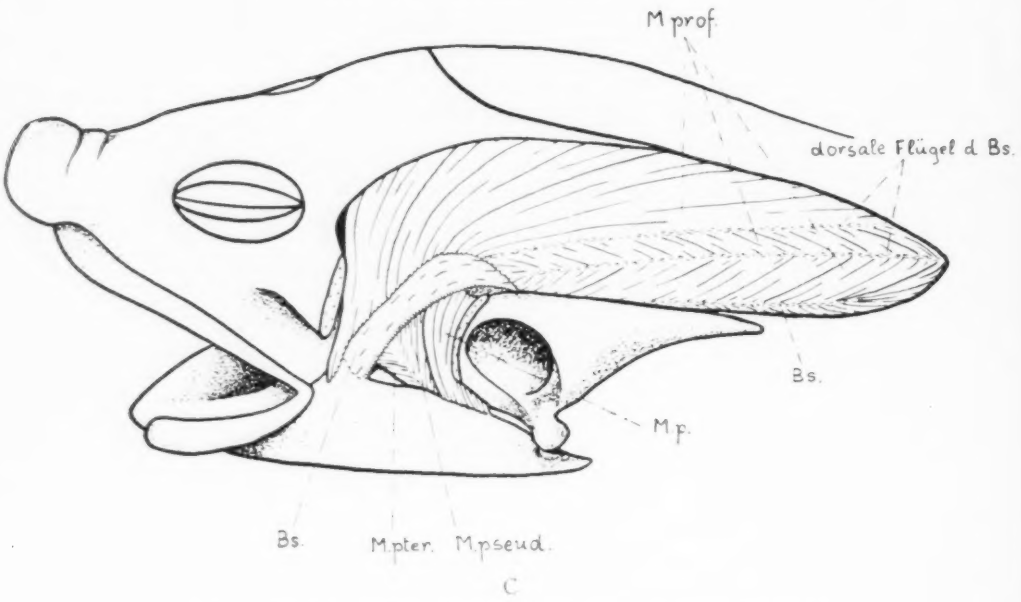


Abb. 3. Atypische Portion des M. adductor mand. externus profundus.
A *Clemmys caspica*. B *Cuora amboinensis*. C *Amyda sinensis*. Gliederung des typischen M.add.mand.ext. profundus und Topik des Adductor mand. posterior und internus.

sehne. Eine kleine medio-rostral der P. profunda gelegene Partie (P.prof.atyp.) wurde auch hier gefunden. Sie liegt lateral des Add. internus und medial der Binnensehne, entspringt in der dorsalen Bucht der oberen Schläfengrube, die vom Parietale und Prooticum gebildet wird, weiters am ventro-medialen Teil des Prooticum und grenzt caudal an den Adductor posterior. Die Fasern dieser Portion ziehen ventrad und setzen bei einem der drei untersuchten Tiere nur an der Gaumenhaut medial vom Coronoid an; beim zweiten Exemplar setzt der Hauptteil der Fasern medial am unteren Abschnitt der Binnensehne an und nur wenige Fasern strahlen in die Gaumenhaut ein; beim dritten Tier hingegen strahlt der Grossteil der Fasern in die Gaumenhaut ein und nur die caudalen Fasern inserieren an der Binnensehne. Die Variabilität des Muskelansatzes tritt an jedem der drei Köpfe beidseitig gleich auf.

b) M. adductor mdb. p o s t e r i o r: Dieser einheitliche Muskel, der eine selbständige Portion des Adductor mandibulae darstellt, bekam seinen Namen mit Rücksicht auf seine Lage zum Ramus mandibularis trigemini, dem er caudal anliegt. Seine Abgrenzbarkeit gegen die anderen Adductoren ist immer deutlich. Er ist ein einfacher Muskel, der nur einmal eine leichte Tendenz zur Bildung zweier Ursprungsköpfe zeigt (*Pelusios*) und bedeutend schwächer als jeder der beiden anderen Adductoren in seiner Gesamtheit. Der Muskel liegt caudo-medial der P. superficialis, medial der P. media des Add. externus

VOL 34 195

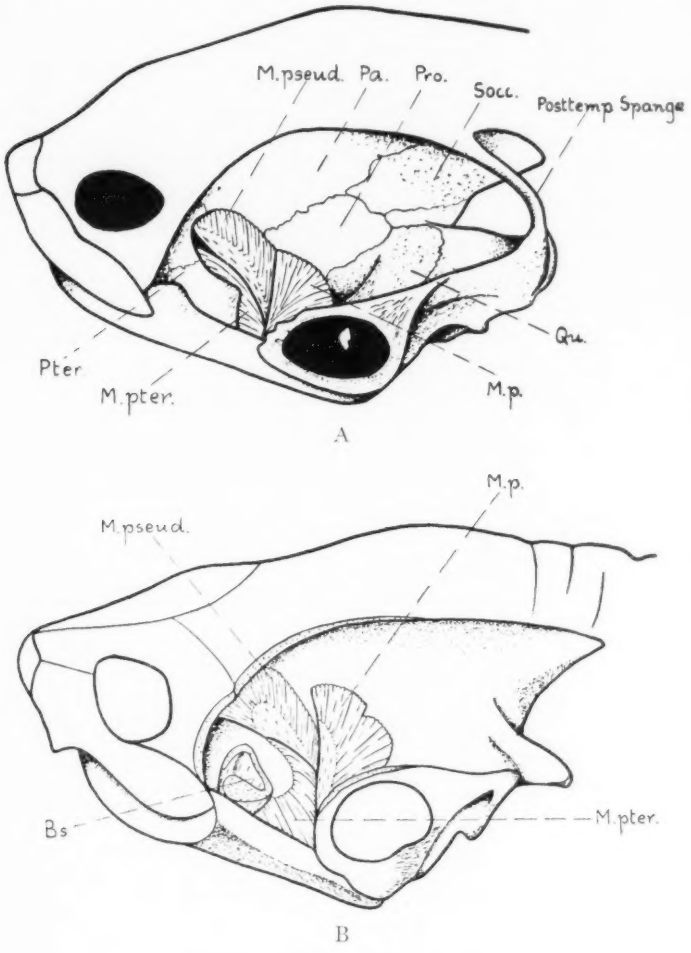


Abb. 4. M. adductor mand. posterior.
A *Batrachemys nasuta*. Typisches Verhalten. B *Pelusios niger*. Atypisches Verhalten.

und caudo-lateral der P. pseudotemporalis des Add. internus. Knapp rostral seines Ursprunges befindet sich das Foramen V; der R. mandibularis grenzt den Muskel gegen die P. pseudotemporalis ab.

Der Adductor posterior entspringt breit an der Rostralkante des Prooticum und am Rostro-Medialteil des Quadratum. Seine Fasern ziehen konvergierend steil nach ventral, wobei die medialen Fasern sich in die von Prooticum und Quadratum geformte Bucht schmiegen. Der Muskel inseriert fleischig bei *Caretta, Chelydra, Chelodina, Batrachemys,* rostral sehnig, caudal fleischig bei *Testudo* und *Terrapene,* oder sehnig bei *Pseudemys, Chrysemys, Malaclemys*

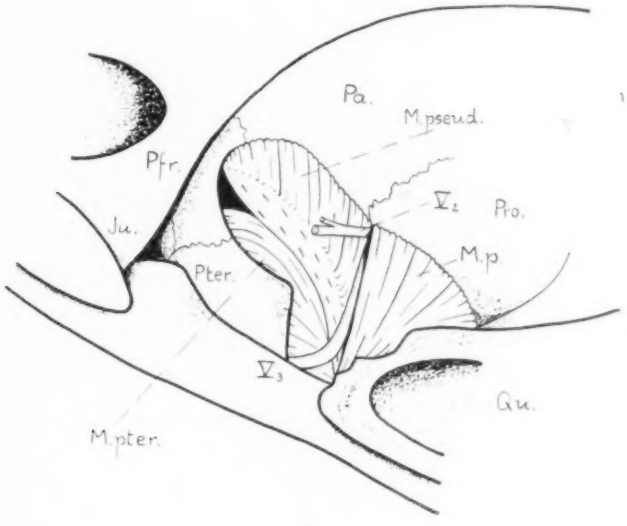
und *Emys* dorso-medial am Hinterrand der Mandibel, zwischen der Fossa primordialis (Fossa praearticularis-FUCHS, Ostium superius inframaxillaris-HOFFMANN) und der Articulationsstelle, entsprechend dem Bau des Unterkiefers, am Goniale (Postoperculare-FUCHS) bei *Chelydra* und *Chelodina*, oder am Supraangulare bei *Caretta, Pseudemys, Chrysemys, Emys, Terrapene* und *Batrachemys*. Bei *Malaclemys, Clemmys* und *Testudo* liegt der Ansatz am Articulare und Supraangulare. Bei *Dermochelys* und *Cuora* inseriert der Muskel dorsal am MECKEL'schen Knorpel, der hier caudo-medial aus der Mandibel heraustritt. Der Muskel ist bei *Kinosternon* und *Sternotherus* recht kräftig und reicht weit nach medial. Sein Ursprung erstreckt sich vom Gebiet ventral des For. V über die Ventralfläche des Prooticum bis einschliesslich zur Rostro-Medialfläche des Quadratum, medial der P. superficialis des Add.ext. Die Muskelfasern ordnen sich um eine Sehne an, die einigen von ihnen zum Ansatz dient und selbst medial am Articulare inseriert, wo auch die restlichen Fasern ansetzen. Der Add. posterior entspringt bei *Pelusios* als auffallend breiter Muskel mit zwei, allerdings nicht deutlich getrennten Köpfen, von denen der mediale Kopf caudal der P. pseudotemporalis, zum Teil noch am Parietale, teils schon am Prooticum, der laterale Kopf am Ventralabschnitt des Prooticum und entlang der Medio-Rostralfläche des Quadratum entspringt. Der Muskel ist hier wohl flächenmässig ausgedehnt, doch gewinnt er kaum an Stärke; er geht rostro-lateral in eine Sehne über, die am Goniale ansetzt. Bei *Amyda* entspringt der Muskel an der Rostralfläche des Prooticum. Seine Fasern laufen leicht ventro-caudalwärts und setzen am Caudalabschnitt des Goniale an. Der Adductor posterior besitzt keinerlei sehnige Differenzierung.

Die Versorgung des Muskels erfolgt durch caudo-medial vom $R.V_3$, oder vom Nervus externus, zuweilen auch von beiden abgehende Nerven, die jedoch niemals mit den Internusnerven in Verbindung stehen.

c) M. adductor mdb. i n t e r n u s: Der Adductor internus setzt sich aus zwei Portionen zusammen, (P. pseudotemporalis und P. pterygoidea), die wegen ihres meist gemeinsamen Ansatzes, wegen ihrer Lage medial vom R. mandibularis und meist auch R. maxillaris (R. supramaxillaris-HOFFMANN, R. maxillaris infraorbitalis-FUCHS) und aus ontogenetischen Erwägungen als Einheit bezeichnet werden. Der Add. internus füllt den noch verbliebenen, ventro-medialen Raum der unteren Temporalgrube aus, kann sich aber auch, wie bei *Caretta*, ziemlich weit rostrad an das Interorbitalseptum ausdehnen. Die Zusammengehörigkeit der Internusportionen und ihre bei den Schildkröten besonders enge Bindung wird, abgesehen von dem fast stets gemeinsamen Ansatz beider Portionen (nur bei *Caretta, Dermochelys, Chrysemys* und *Graptemys* inserieren P. pseudotemporalis und P. pterygoidea getrennt), durch den Innervationsbefund noch unterstrichen. In der Mehrzahl der Fälle entspringen die die beiden Partien versorgenden Nerven gemeinsam, seltener getrennt, immer jedoch medial, selbständig vom $R.V_3$. Der Ursprung der beiden Nerven liegt

stets im obersten Abschnitt des R.V_3. Nur bei *Dermochelys* entspringt der N. pter. im unteren Drittel des R. mandibularis.

Die P. pseudotemporalis (Abb. 5) mit ihrem fächerartig ausgebreiteten Ursprung am vorderen Ventro-Lateralabschnitt, bzw. Proc. descendens des Parietale, ist nie besonders kräftig entwickelt. Eng an das Parietale geschmiegt, zieht der Muskel, sich ventral verjüngend, fast immer medial des breiten, bandartigen R. maxillaris zur Mandibel. Nur bei *Dermochelys* und *Testudo* liegt der Muskel lateral vom R.V_2. Es kommt häufig vor, dass der Nerv von caudal in den Muskel läuft und von einem caudalen Muskelbündel von wechselnder Stärke lateral bedeckt wird (*Chelydra, Kinosternon, Malaclemys, Clemmys, Terrapene*), doch ändert dies an der Definition der Portion nichts, zumal ihre Lagebeziehung zum R. mandibularis davon immer unberührt bleibt. Die schwache Portion besitzt durchwegs rostro-lateral eine oberflächliche Aponeurose — diese fehlt bei *Dermochelys* — welche rostral einen Umschlagsrand besitzen kann (*Emys, Pelusios*) und mit ihrer Caudalfläche den Fasern der P. pseudotemporalis zum Ansatz dient. Nur bei *Pseudemys* setzen einzelne Fasern selbständig neben der Sehne an. Die Sehne inseriert in der Mehrzahl der Fälle am Goniale (*Kinosternon, Sternotherus, Malaclemys, Clemmys, Emys, Cuora, Amyda*). Mit der verschiedenen Ausbildung der Deckknochen dieser Region wechselt der Ansatz der Sehne. Er liegt bei *Terrapene* am Goniale und Caudalfortsatz des Coronoid, bei *Pelusios* am Rostralabschnitt des Articulare und bei *Batrachemys* am Dorsalkamm des Operculare. Bei *Dermochelys* entspringt die P. pseudotemporalis am Medio-Rostralteil des Prooticum und an der hier knorpeligen Hirnkapsel und setzt, ohne Sehnenbildung, dorsal



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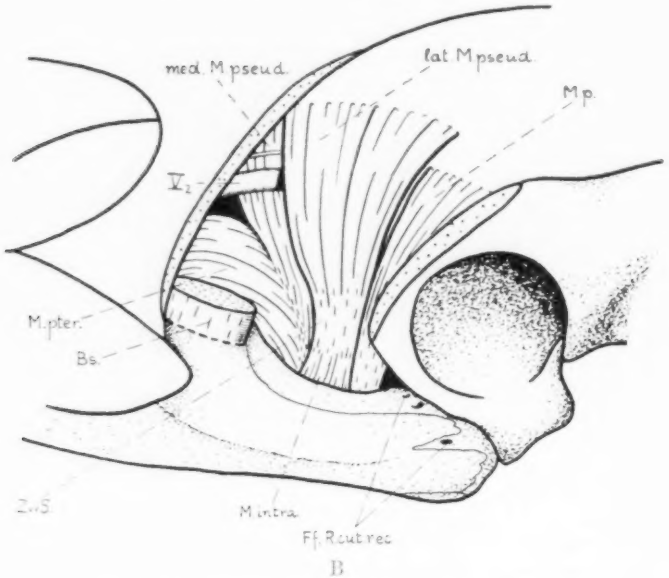


Abb. 5. M. adductor mand. internus pseudotemporalis.
A *Batrachemys nasuta*. Typische Form. B *Pseudemys scripta troostii*. Teilung in laterale und mediale Portion durch hindurchziehenden R.V$_2$; Bildung einer Zwischensehne von der lateralen Portion zum M. intramandibularis.

der P. pterygoidea und rostral vom Add. posterior, am MECKEL'schen Knorpel an. Der Muskel entspringt bei *Caretta* am Rostralteil des Parietale und am Caudalteil des Interorbitalseptum. Er wird lateral von einer dorso-ventral laufenden Sehne bedeckt, an der seine Fasern ansetzen. Die Sehne zieht in die Fossa primordialis, wo sie den Fasern eines neuen Muskels — M. intramandibularis — der am Boden der Fossa ansetzt, zum Ursprung dient. Bei *Chelydra* ist der Muskel durch eine besondere Sehnenausbildung charakterisiert. Der Ursprung der P. pseudotemporalis liegt am Rostro-Ventralabschnitt des Parietale und am Rostro-Medialteil des Prooticum. Ihre Sehne ist im Querschnitt „T"-förmig, die Lage der Sehne so, dass die Flächen des einen Blattes — „laterales Blatt" — nach lateral und medial, die Flächen des anderen Blattes — „mediales Blatt" —, das medial vom „lateralen Blatt" abgeht, nach caudal und rostral weisen. Die Fasern der P. pseudotemporalis inserieren an der Lateralfläche des „lateralen Blattes", an der Medialfläche des „lateralen Blattes", caudal vom „medialen Blatt" und an der Caudalfläche des „medialen Blattes". An den übrigen Flächen setzen die Fasern der P. pterygoidea an. Die Sehne inseriert medial am Goniale. Der bei *Pseudemys* kräftigere Muskel wird durch den Verlauf des R.V$_2$ in zwei Portionen geteilt. Beide Portionen haben ein gemeinsames Ursprungsgebiet, da die Trennung in eine laterale und

VOL 34 195

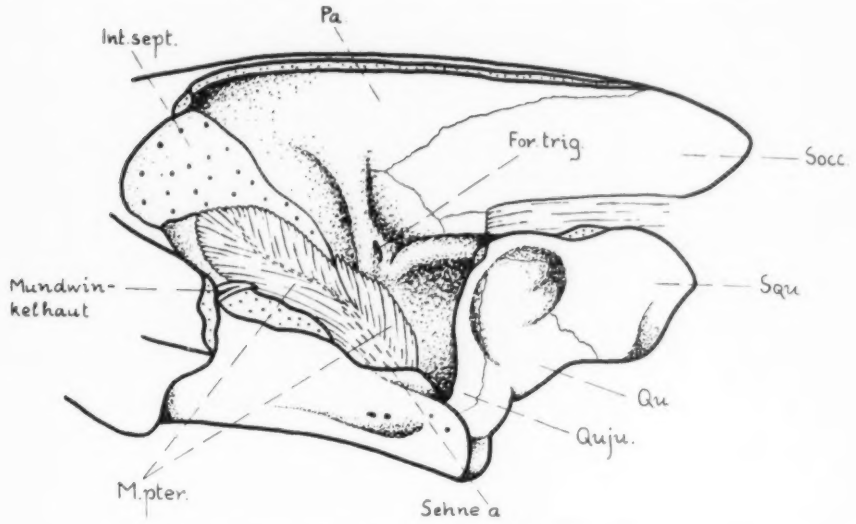


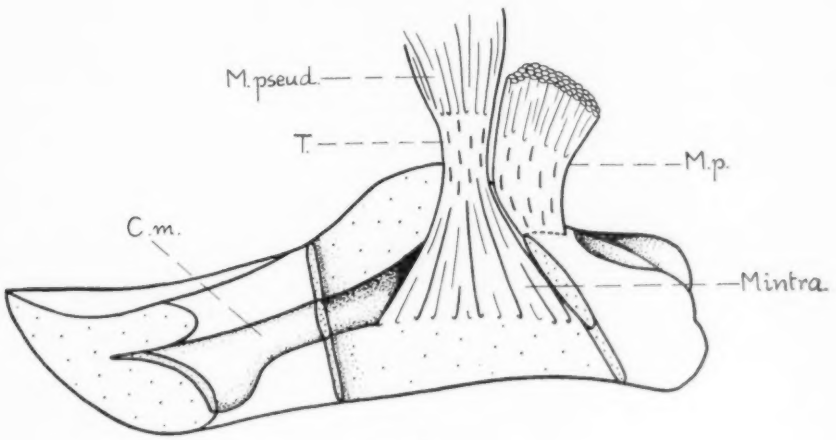
Abb. 6. M. adductor mand. internus pterygoideus von Caretta caretta.

eine mediale Portion erst auf der Höhe des R.V$_2$ erfolgt. Die l a t e r a l e Portion entspringt am Proc.desc. des Parietale. Ihre Fasern ziehen steil ventrad und gehen, relativ weit dorsal der Mandibel, in eine kurze Sehne über, die auch noch dorsal der Mandibel, den Fasern des M. intramandibularis zum Ursprung dient. Die m e d i a l e Portion wird in ihrem rostralen Bereich von einer Sehne bedeckt. Die Muskelfasern entspringen am Proc.desc. und setzen zum Hauptteil an der Caudalfläche dieser Sehne an. Nur wenige Fasern inserieren selbständig neben der Sehne, rostro-medial vom Add. posterior, am Dorsalrand des Goniale. Die mediale Portion ist also nicht an der Bildung des M. intramandibularis beteiligt. Bei *Chrysemys* und *Graptemys* geht der einheitliche Add.int.pseudotemporalis unter Bildung einer Zwischensehne in den M. intra. über. Die P. pseudotemporalis liegt bei *Testudo* lateral vom R.V.$_2$ und medial vom N. ad angulum oris (R. buccinatorius-Bojanus, Hoffmann, Fuchs). Er entspringt zweiköpfig, mit einem schwächeren latero-caudalen und einem stärkeren medio-rostraden Kopf, von denen ersterer dorsal, letzterer rostral vom For.V am Parietale entspringt. Lateral und rostral sehnig, setzen beide Portionen gemeinsam medial am Goniale an. Die Fasern dieser Portion entspringen bei *Chelodina* am Ventralabschnitt des Parietale, ziehen nach caudoventral und setzen an einer Sehne an, die den Muskel rostrolateral bedeckt. Die Sehne zieht in die Fossa prim., wo sie lateral an der Cartilago meckeli inseriert. Einige der medialen Fasern setzen selbständig, dorsal am Meckel'schen Knorpel an.

Die P. p t e r y g o i d e a des Add. internus (Abb. 6) bildet die ventrale Begrenzung der unteren Temporalgrube. Als Ursprungsgebiet dient ihr stets

die Dorsalfläche des Pterygoid, doch kann der Ursprung weit in die Orbita, bis zum Palatinum vorgeschoben sein, wie bei *Caretta*, bei der sich auch die P. pseudotemporalis weiter rostrad ausbreitet als bei den anderen Schildkröten. Die P. pterygoidea, kräftiger als die P. pseudotemporalis, zieht anfangs caudalwärts, erst allmählich wenden sich die Fasern nach caudo-ventral und inserieren an der Rostralfläche der Aponeurose der P. pseudotemporalis (Ausnahmen: *Dermochelys*, *Caretta*), manchmal zusätzlich an der Gaumenhaut (*Kinosternon*, *Terrapene*); bei *Sternotherus* liegt der Ansatz an der Sehne, an der Gaumenhaut und am Goniale. Die bei *Dermochelys* sehr bescheidene Portion wird caudo-lateral von den rostralen Fasern der P. pseudotemporalis bedeckt. Der Muskel entspringt fächerförmig ausgebreitet auf der Dorsalfläche und Caudalkante des Pterygoid und setzt, mit seinen ventralen Fasern leicht schnig, medial an der Mandibel, ventral der P. pseudotemporalis und rostral des Add. posterior, am MECKEL'schen Knorpel und am Goniale an. Bei *Caretta* liegt die kräftigere Portion auch unmittelbar ventral der sich ziemlich weit nach rostral erstreckenden P. pseudotemporalis. Der Ursprung der dorsalen Fasern ist weit in die Orbita vorgeschoben und reicht bis an die Dorsalfläche des Palatinum und den Ventralabschnitt des Septum interorbitale; er erstreckt sich aber auch caudal bis an den ventralen Teil des Proc.desc. des Parietale. Die dorsalen Fasern inserieren lateral an einer Sehne a. Die ventralen Fasern entspringen am Lateralrand und gesamten ventralen Gebiet des Pterygoid. Der Muskel umschliesst oben erwähnte Sehne a, die im Querschnitt etwa „T"-förmig erscheint und den gesamten dorsalen und einem Teil der ventralen Fasern zum Ansatz dient. Ein Teil der ventralen Fasern — rostraler Teil — inseriert mit wenigen Fasern an der Gaumenhaut, mit den restlichen Fasern dorsal an der Sehne b, die den Muskel ventral bedeckt und fleischig am Goniale. Die Sehne a setzt am medialen Rand der Fossa primordialis an, die dem Muskel ventral anliegende Sehne b inseriert medial am Articulare. Innervationsmässig ist die Trennung der beiden Internusportionen bei *Caretta* nicht so klar festgelegt, da die P. pseudotemporalis neben ihrem eigenen sie versorgenden Nerv noch eine Komponente vom N. pterygoideus erhält. Die Fasern nehmen bei *Chelydra* ihren Ursprung an der Lateral- und Dorsalfläche des Pterygoid, einige auch am Caudalende des Palatinum. Der Ansatz erfolgt an der Rostralkante des „lateralen Blattes", an der Medialfläche des „lateralen Blattes" rostral vom „medialen Blatt" und an der Rostralfläche des „medialen Blattes" der „T"-förmigen Sehne, die der P. pseudotemporalis und pterygoidea angehört. Bei *Pseudemys* setzt der Muskel an der die mediale Portion des zweigeteilten Add.int.pseudotemporalis umgebenden Sehne an. Bei *Testudo* liegt der Ansatz teils an der Sehne der P. pseudotemporalis, teils an der die P. pterygoidea ventral umgebenden Sehne, die am Goniale, ventral der P. pseudotemporalis, inseriert.

d) M. intramandibularis (Abb. 7): Dieser bisher bei den Schildkröten noch unbekannte Muskel, tritt nur bei wenigen Gattungen — *Caretta, Pseudemys, Chrysemys, Graptemys* — in sehr ähnlicher Ausbildung auf. Er ist ein gut abgrenzbarer Muskel, der mittels einer Sehne mit der P. pseudotemporalis des Add. internus in Beziehung steht. Versorgt wird der Muskel durch 1—2 zarte Nervchen, die von einem, vom Ramus alveolaris abgehenden Nerv — R. intermandibularis caudalis — entspringen.



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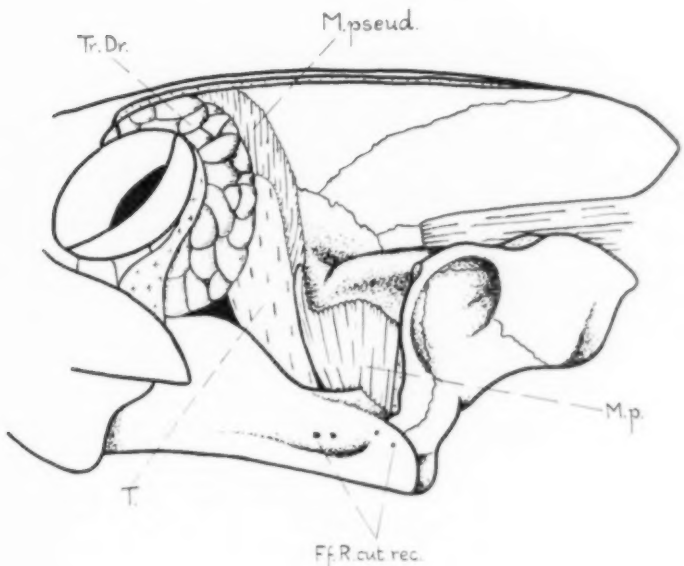

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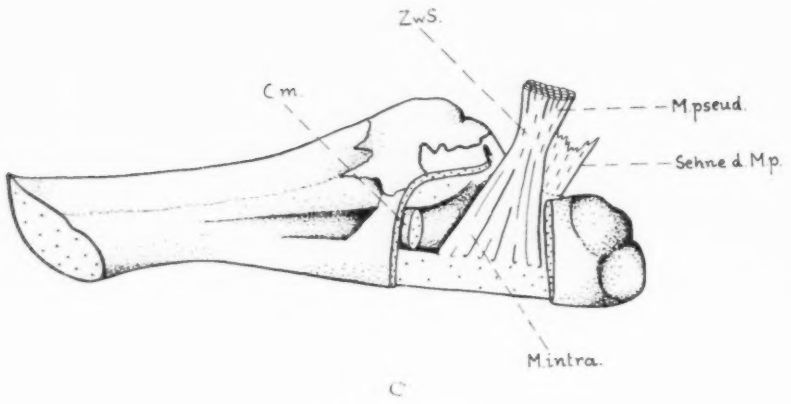
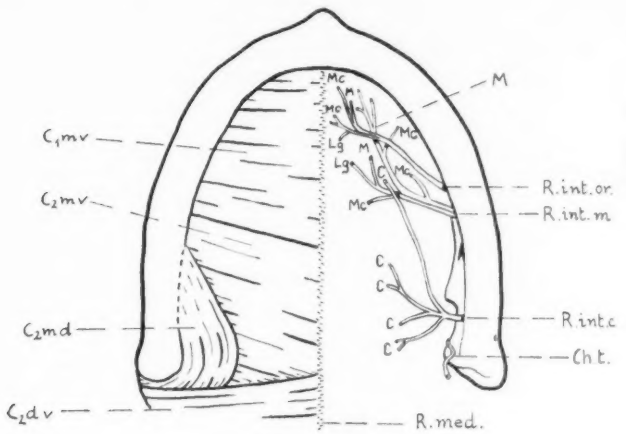


Abb. 7. M. intramandibularis.
A *Caretta caretta*. Medialansicht des M. intramandibularis. B *Caretta caretta*. Lateralansicht des M. adductor mand. int. pseudotemporalis mit Insertionssehne, deren Medialfläche Ursprungsgebiet des M. intramandibularis ist. C *Pseudemys scripta troostii*. M.add.-mand.it. pseudotemporalis und M. intramandibularis durch Zwischensehne getrennt.

Bei *Caretta* entspringen die Fasern des M.intra. innerhalb der Fossa primordialis, medial an der sich ventral leicht verjüngenden Sehne der P. pseudotemporalis; die Fasern des M.intra., der sich leicht auffächert, setzen am Boden der Fossa, lateral der Cartilago Meckeli an. Die Sehne inseriert, lateral vom Muskel, ebenfalls am Boden der Fossa. Bei *Pseudemys* gehen die Fasern der lateralen Portion des Add.int.pseudotemporalis, ziemlich weit dorsal der Mandibel, in eine kürzere Sehne über, die sich, noch vor Eintritt in die Fossa prim., auffasert und einen neuen Muskel, den M. intramandibularis, bildet. Der Muskel zieht, sich ein wenig verbreiternd, in die Fossa und inseriert, lateral des MECKEL'schen Knorpels, am Boden der Fossa primordialis. Bei *Chrysemys* und *Graptemys* geht die P. pseudotemporalis, unter Bildung einer Zwischensehne, in den M.intra. über, welcher bei diesen Tieren sein Ansatzgebiet noch eine kleine Strecke weiter rostrad als bei den anderen Gattungen in den hinteren Teil des Canalis primordialis ausdehnt.

e) M. intermandibularis (Abb. 8): Der ventrale Constrictor ist bedeutend einfacher gebaut als die übrige Kiefermuskulatur. Der rostrale Teil dieses dünnen, flächenhaften Muskels — Pars oralis ($M.C_{1}v$) — wird von einem Ast des N. trigeminus innerviert, während der hintere Teil — Pars caudalis ($M.C_{2}v$) — der caudal an den M. sphincter colli grenzt, vom N. facialis versorgt wird. Die beiden Partien, die manchmal auch bei sorgfältigster Präparation kaum durch verschiedene Faserführung voneinander zu unterscheiden sind (Unterscheidung nur mit Hilfe des Innervationsbefundes bei *Dermochelys*, *Caretta*, *Chelydra*), breiten sich, beiderseits an der Medialfläche der Mandibel entspringend, als dünne, oberflächliche Muskelschicht über das ganze Gebiet

zwischen den Unterkieferästen aus, wobei sich die Pars oralis immer auf einen flächenmässig kleineren Teil dieses Gebietes beschränkt als die Pars caudalis. Das Ursprungsgebiet der Fasern liegt knapp dorsal der Cartilago Meckeli, auf der Höhe des Coronoid etwas nach dorsal verschoben, hinter diesem wieder auf ursprünglicher Höhe und endet wenig caudal des Foramen R. intermand. caudalis (Ostium canalis mylohyoideus—HOFFMANN). Die Fasern des M.C$_{IV}$



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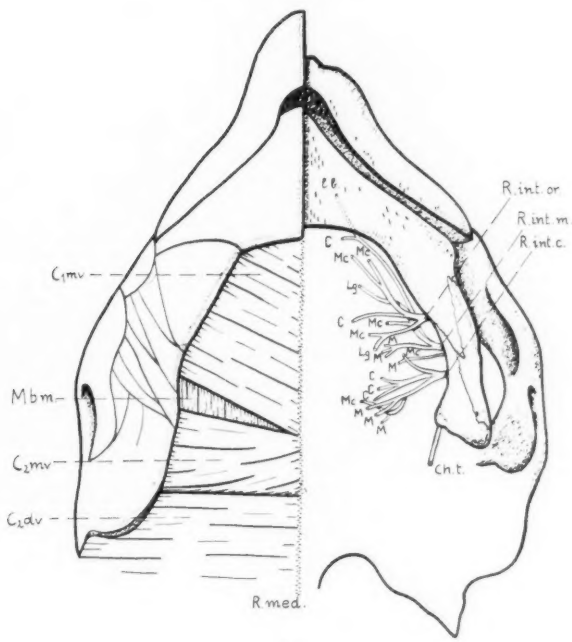

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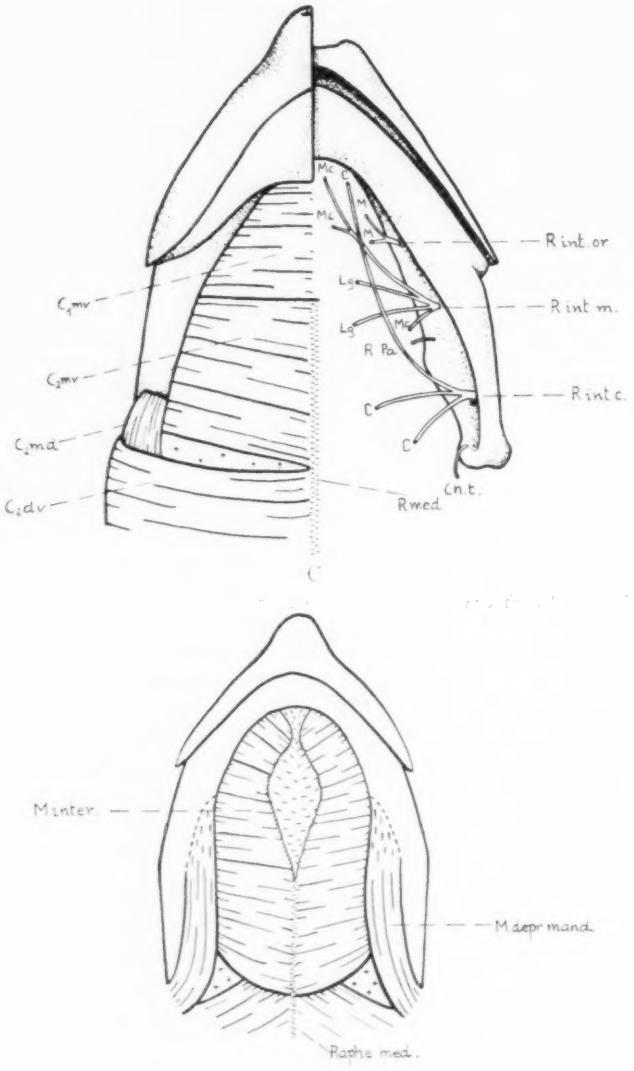


Abb. 8. M. intermandibularis mit Darstellung der Unterkiefernerven.
A *Batrachemys nasuta*. Durchlaufende Raphe. Übergang von C_1mv in C_2mv. B *Pelusios niger*. C_1mv und C_2mv durch Spalt getrennt, durchgehende Raphe. C *Pseudemys scripta troostii*. Raphe nur im Bereich des C_2mv. D *Chelodina longicollis*. Übergang von C_1mv in C_2mv. Differenzierung der Raphe.

inserieren an einer feinen, sehnigen Längsraphe — Raphe medialis (RUGE) — (*Dermochelys, Caretta, Chelydra, Batrachemys, Amyda*), die sich auch zu einer ansehnlichen Aponeurose verbreitern kann (*Chelodina*), aber auch oft

VOL. 34 1953

nicht bis zur Symphyse durchläuft (*Kinosternon, Sternotherus, Pseudemys, Chrysemys, Malaclemys, Clemmys, Emys, Cuora, Terrapene*), wobei in diesem Fall der rostral der Raphe gelegene Muskelabschnitt dem M. intermandibularis oralis ($M.C_{1}v$) entspricht. Bei *Testudo* reichen rostral Muskel und Raphe nicht ganz bis zur Symphyse, wodurch in deren Bereich die Fasern der Mundbodenmuskulatur sichtbar werden. Im übrigen gleicht der Muskel dem von *Dermochelys, Caretta, Chelydra, Batrachemys* und *Amyda*. Durch eine aussergewöhnlich starke Verbreiterung der sehnigen Raphe medialis wird bei *Chelodina* der intermandibulare Muskel, besonders in dessen vorderem Abschnitt, stark beiderseits nach lateral abgedrängt. Die Raphe medialis läuft bis zum ungefähren Hinterende der P. oralis normal, also als dünnsehnige Mittelleiste, an der beiderseits die Fasern der P. caudalis ansetzen. Sie verbreitert sich darauf allmählich, um rostral wieder schmäler zu werden, so dass die rostralen Fasern der P. oralis in der Mediane fast wieder zusammenstossen. An ihrer Insertionsstelle, an der Unterkieferspitze, erscheint die zu einer sehnigen Platte umgewandelte Raphe wieder beträchtlich breit, so dass aus dem Gebiet der Symphyse Muskelfasern des M. intermandibularis überhaupt ausgeschlossen sind. Auffallend ist auch der hier stark sehnige und weit rostrad reichende Ansatz des M. depressor mandibulae, der medio-ventral an der Mandibel inseriert. Die Pars caudalis reicht bei *Pelusios* so weit nach caudal, dass sie etwas mehr als die Hälfte der zwischen den Unterkiefern eingeschlossenen Fläche bedeckt. Der $M.C_{1}v$ entspringt medial an der Mandibel, dorsal des MECKEL'schen Knorpels, hat eine leicht medio-caudale Faserrichtung und setzt an der Raphe medialis an. Der Muskel ist durch einen besonders grossen Zwischenraum, in dem man die dorsal laufenden Fasern der Mundbodenmuskulatur sieht, vom $M.C_{2}v$ scharf getrennt und stösst mit diesem nur im Ansatzgebiet zusammen.

Die Pars oralis — $M.C_{1}v$ — des M. intermandibularis wird bei den meisten Cheloniern durch den R. intermandibularis oralis innerviert. Bei *Caretta* und *Chelodina* wird der Muskel zur Gänze vom R. intermand. medius versorgt. Bei *Pelusios* kommt es zu Doppelinnervation durch den R. intermand. caudalis und R. intermand. medius; ähnlich bei *Batrachemys*, bei der der Muskel durch den R. intermand. medius und R. intermand. oralis versorgt wird. Nähere Angaben über die drei vom R. alveolaris abgehenden Nervenzweige vgl. S. 276.

II. INNERVATION.

Bei der Besprechung des Nervus trigeminus verzichte ich auf eine genaue Darstellung des R. ophthalmicus und R. maxillaris, und beschreibe diese rein sensiblen Elemente nur insoweit, als es für die allgemeine Orientierung notwendig erscheint.

Der N. trigeminus bildet, noch innerhalb der Schädelkapsel, zwei Ganglien aus; das kleinere, unscheinbarere Ganglion ophthalmicum, von dem der R. ophthalmicus abgeht,

liegt knapp caudo-medial vom grösseren Ganglion maxillo-mandibulare (Ggl. GASSERI nach GAUPP 1896, LUTHER 1914, LAKJER 1926, Ggl. semilunare nach LUBOSCH 1933), von dem die Rr. maxillaris und mandibularis abgehen. Das Ggl. ophthalmicum ist grösstenteils mit dem Ggl. maxillo-mandibulare verschmolzen, so dass es nur als kleinere Anschwellung desselben wahrnehmbar ist. Nur bei einem der drei untersuchten Exemplare von *Chelodina* fand ich als besondere Abnormität das Ggl. trigemini fast zur Gänze aus der Schädelkapsel in die Temporalgrube verlagert, so dass sich nur sein caudo-dorsalstes Ende noch im Foramen trigemini befand.

Der R.V$_1$ verlässt durch ein eigenes Foramen, rostro-medial vom For. V$_2$+V$_3$, das Cavum cranii, nur bei *Dermochelys* tritt R.V$_1$ gemeinsam mit R.V$_2$+R.V$_3$ aus dem For.trig. in die untere Temporalgrube aus — bei diesem Tier ist keine Andeutung eines Ggl. ophthalmicum erkennbar — und zieht, lateral der Adductor-internus-Muskulatur, zur Orbita.

Der R.V$_2$ tritt gemeinsam mit dem Ramus V$_3$, von diesem bereits getrennt, durch das For.trig. in die Schläfengrube. Bei den Exemplaren von *Chelodina*, bei welchen das Ganglion innerhalb der Schädelkapsel liegt, treten gemeinsam mit R.V$_2$ und R.V$_3$ auch die zwei Nn. pseudotemporales, die beiden Nn. pterygoidei und der N.prof.+med. aus dem Foramen aus, während diese Äste im Normalfall direkt vom R.V$_3$ erst mehr oder weniger distal nach dessen Austritt aus dem For.V. abgehen. R.V$_2$, der kräftigste Nerv nach R.V$_3$, biegt nach Verlassen des Foramens scharf rostrad und zieht, sich mehrfach verzweigend, zur Orbita. Er läuft medial vom Add.ext. profundus, lateral vom Add.int. pseudotemporalis, letzterem eng anliegend. Oft dringt er von caudal in die P. pseudotemporalis ein, und tritt gleich, nur von ein paar caudalen Muskelfasern bedeckt, wieder aus dem Muskel heraus (*Chelydra, Kinosternon, Malaclemys, Terrapene, Clemmys*); nur sehr selten läuft R.V$_2$ medial der P. pseudotemporalis (*Dermochelys, Testudo*).

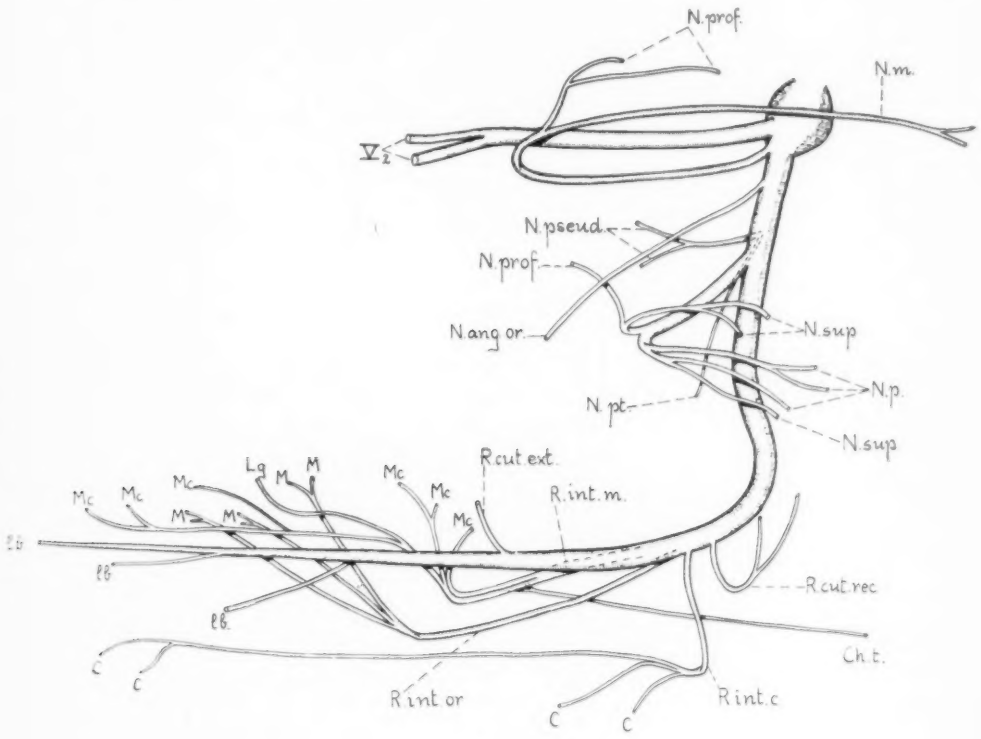
Ramus V$_3$ läuft in der Regel geradlinig, nur bei *Dermochelys, Malaclemys* und *Pseudemys* läuft er mehrfach leicht gebogen, ziemlich steil dorso-ventral, dabei leicht von medial nach lateral, und in nach rostral offenem Bogen zieht er schliesslich in die Fossa primordialis, um von hier an als Ramus alveolaris (R. alveolaris inferior nach FUCHS, R. inframaxillaris nach HOFFMANN) horizontal im Canalis primordialis, in der Mandibel, zur Kieferspitze zu führen. Der Ramus mandibularis führt sowohl motorische als auch sensible Fasern. Er versorgt mit den von ihm abgehenden Aesten den Adductor mandibulae, als Ramus alveolaris, den Constrictor I ventralis und, wenn vorhanden, den M. intramandibularis. Ferner versorgt er sensibel die Mundwinkelhaut (nur bei *Dermochelys* geht dieser sensible Ast vom R.V$_2$ ab, bei *Chelodina* entspringt er direkt vom Ggl. maxillo-mandibulare), die den Unterkiefer bedeckende Haut und, im Gebiet zwischen den Unterkieferästen, Haut, Sublingualdrüsen, Zunge und Mundschleimhaut, wobei an der Versorgung von Zunge und Mundschleimhaut auch die Chorda tympani des N. VII beteiligt ist. Auch in topographischer Hinsicht gewährt der Verlauf des R.V$_3$ günstige Anhaltspunkte zur Einteilung der Muskulatur. Rostral vom M. add. posterior, medial vom M. add. externus und lateral vom M. add. internus laufend, bestimmt der R.V$_3$ die Einteilung der Kaumuskulatur. Auch die Art der Innervierung der Adductorpotionen ist für deren Unterscheidung von grosser Wichtigkeit. So entspringen die Nerven für den Add. internus medial, den Add.

VOL. 34 1953

externus lateral und für den Add. posterior medio-caudal vom R.V_3, oder für letzteren lateral vom N. externus; manchmal wird der Muskel auch doppelt innerviert.

Wir wollen nun die einzelnen Nerven besprechen (Abb. 9):

N. ad angulum oris: In der Mehrzahl der Fälle — *Chrysemys, Emys, Clemmys, Malaclemys, Kinosternon, Sternotherus, Chelydra* und *Amyda* — entspringt dieser rein sensible Nerv als zweiter Ast rostro-lateral vom R.V_3. Bei *Caretta, Cuora* und *Testudo* entspringt der Nerv als mittlerer von drei Aesten mit gemeinsamer Wurzel, latero-rostral vom R.V_3 in dessen proximalstem Abschnitt. Bei *Pseudemys* und *Terrapene* entspringt der Nerv als erster Ast vom R.V_3 nach dessen Austritt aus dem For. V, gemeinsam mit dem die Pp.med.+ +prof. versorgenden Nerv, der sich nach kurzem, gemeinsamen Verlauf vom N. ad ang. or. löst. Ebenso entspringt er bei *Batrachemys*, jedoch mit den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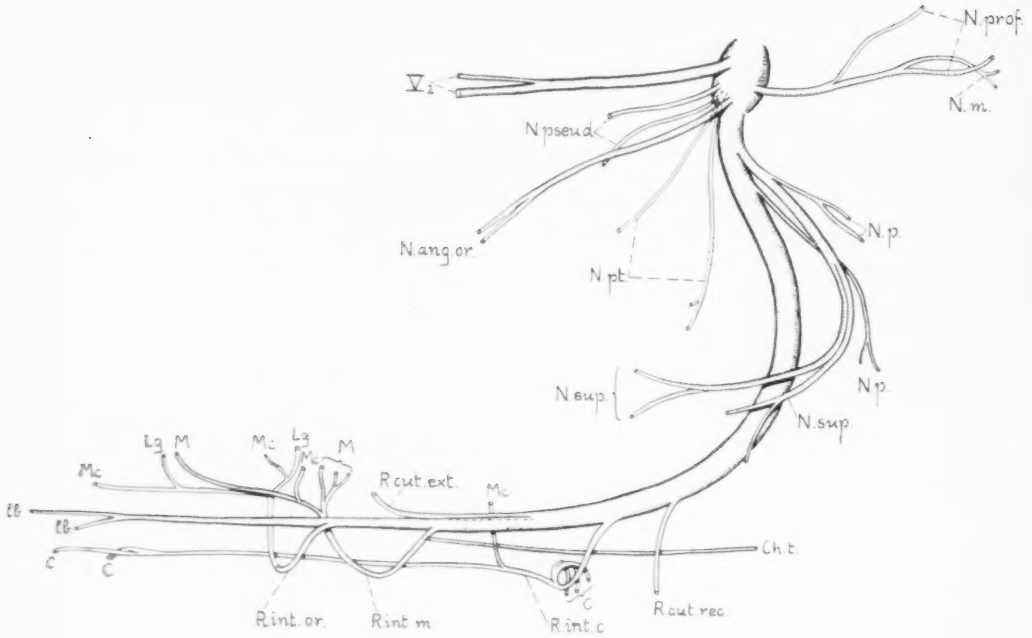

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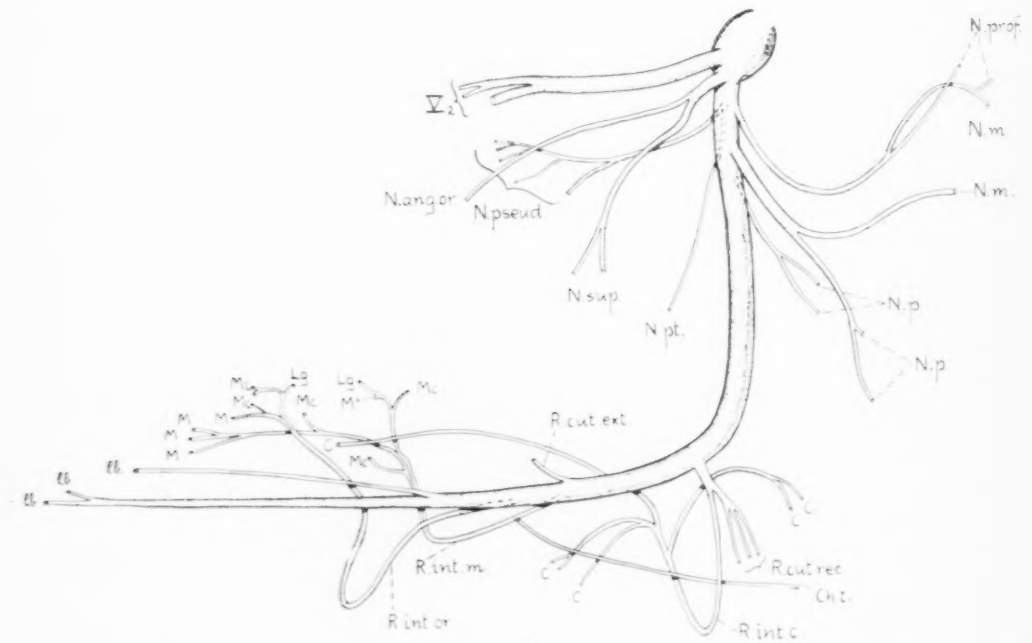

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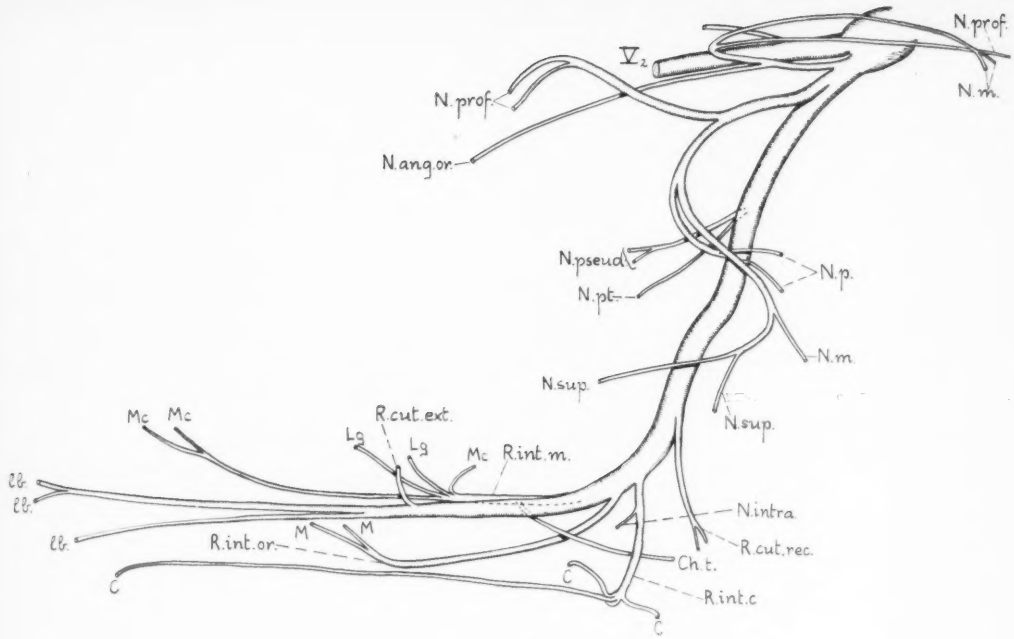
VOL. 34 1953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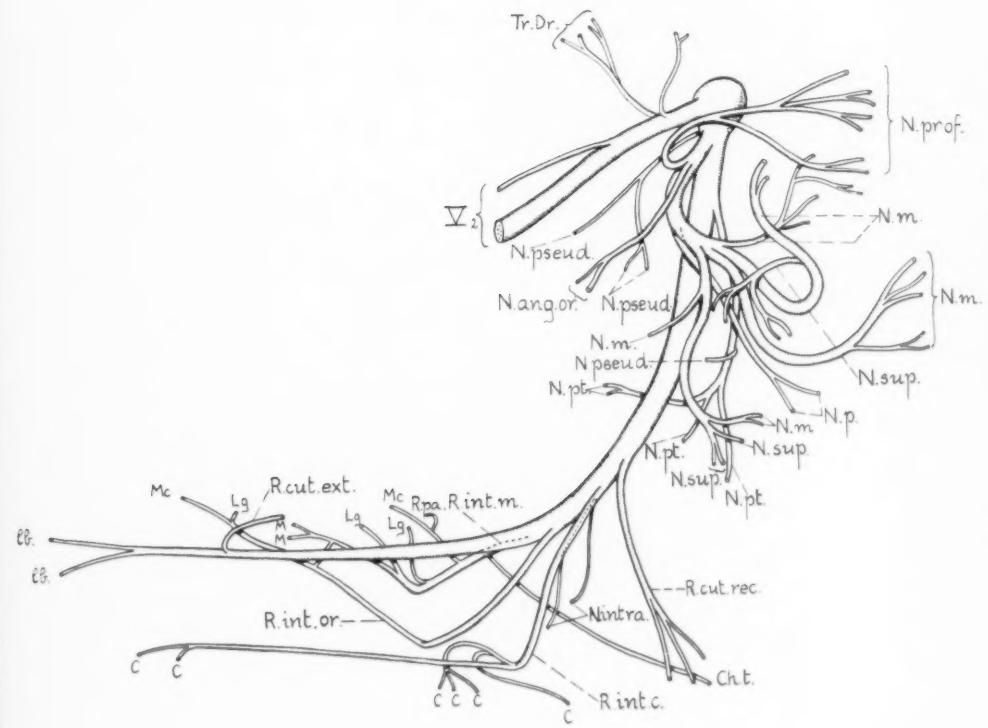
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E

Fasern des N. superficialis verbunden. Bei *Dermochelys* geht der N. ad ang. or. — als Sonderfall — vom sensiblen R.V_2 ab. Bei *Chelodina* entspringt er als dritter Nerv latero-ventral vom Ganglion. Der N. ad angulum oris zieht zwischen der P. pseudotemporalis und der P. profunda nach rostro-ventral — bei *Dermochelys* zieht er medial der P. pseudotemporalis, bei *Caretta* durchbohrt er die P. profunda und P. superficialis in deren Rostralabschnitten — und versorgt die Mundwinkelhaut.

Nn. ad m. add. ext.: Der M. add. ext. wird durch zwei kräftige, lateral vom R.V_3 entspringende Nerven versorgt. Der weiter dorsal abgehende, beträchtlich schwächere Ast versorgt die P. profunda und den caudo-dorsalen Teil der P. media; bei *Pelusios* entspringen diese die beiden Portionen versorgenden Nerven getrennt, knapp untereinander. Der dorsale Ast (N.med.+prof.) geht in der Regel als erster Ast vom R.V_3 ab (*Dermochelys, Chelydra, Kinosternon, Sternotherus, Malaclemys, Chrysemys, Amyda*). Bei *Batrachemys* entspringt er als zweiter Ast, bei *Chelodina* geht er lateral vom Ganglion ab. Bei *Terrapene* und *Pseudemys* läuft der N.med.+prof., mit dem sensiblen N. ad ang. or. verbunden, eine Strecke rostrad, bevor sich seine Fasern von denen des sensiblen Astes lösen. Bei *Cuora* entspringen drei Aeste, mit gemeinsamer, kräftiger Wurzel, rostral vom R.V_3. Als dorsalster dieser Dreiergruppe zweigt der N.med.+prof. ab. Kurz bevor er seine Selbständigkeit erlangt, spaltet er ein schwächeres Aestchen zur Versorgung der medio-rostralen Partie der P. profunda ab. Bei *Emys* entspringt dieser Nerv als erster, aus gemeinsamer Wurzel mit dem N.sup.+post., lateral vom R.V_3. Bei *Testudo* geht der N.med.+prof. aus gemeinsamer Wurzel mit dem N. ad ang. or. und dem N.sup.+med. als dorsalster Ast, rostro-lateral vom R.V_3 ab. Bei *Caretta* wird die P. media und profunda von getrennt entspringenden Nerven versorgt. Diese Nerven entspringen bei diesem Tier von einem kräftigen, lateral vom R.V_3, kurz nach dessen Austritt aus dem For. V abzweigenden Ast, der, sich reich verzweigend, ausserdem die Mundwinkelhaut (enthält also auch N. ad ang. or.), die P. superficialis, den ventro-rostralen Teil der P. media und den M. add. posterior versorgt. Der Nervus med.+prof. zieht, medial an der Binnensehne vorbei, nach ventral, steigt darauf nach dorsal, um im Bogen nach caudal zu laufen und in die P. profunda und media einzutreten. Der zweite, weiter ventral abgehende, ebenfalls den M. add. externus innervierende Ast, ist immer der kräftigste aller vom R. mandibularis abgehenden Nerven. Er verzweigt sich reich und versorgt meist alle Externusportionen; oft führt er auch Fasern zur Teilversorgung des M. add. posterior. Bei *Terrapene, Testudo* und *Amyda* zweigt der Externusast kein Aestchen zur Versorgung des M.add.post. ab. Bei *Cuora, Malaclemys, Emys, Chelodina* und *Pelusios* versorgt dieser Nerv die P. superficialis und den Add.post., bei *Chelydra, Kinosternon, Sternotherus, Pseudemys* und *Chrysemys* die P. superficialis, den ventro-rostralen Teil der P. media, den rostralen Abschnitt der

VOL. 34 1953

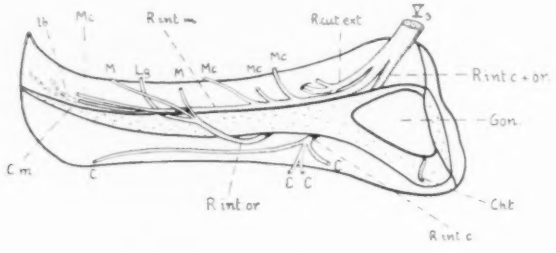
P. profunda und den Add. posterior; bei *Terrapene, Testudo* und *Amyda* versorgt er nur die P. superficialis und die P. media und schliesslich bei *Dermochelys, Caretta* und *Clemmys* die P. superficialis, die P. media und den Add. post. Bei *Batrachemys* innerviert der Ast bloss die P. media und den Add. posterior, während ein eigener Ast, der als proximalster Nerv lateral vom $R.V_3$ entspringt und mit den Fasern des N. ad ang.or. ein kurzes Stück zusammenläuft, die P. superficialis innerviert.

Nn. ad m.add. post: Der M. adductor posterior weist bei *Chelydra, Malaclemys, Clemmys, Chelodina, Batrachemys* und *Pelusios* Doppelinnervierung auf; 1. durch einen mässig starken, caudo-medial bis caudal vom $R.V_3$ selbständig abgehenden und 2. einen schwachen, vom ventralen Externusast abzweigenden Nerv. Diese Doppelinnervierung fehlt bei *Testudo, Amyda* und *Terrapene*, da bei diesen Tieren der ventrale N. externus keinen Ast für den Add.post. abzweigt und bei *Dermochelys, Caretta, Kinosternon, Sternotherus, Pseudemys, Chrysemys, Emys* und *Cuora*, denen der selbständig vom $R.V_3$ entspringende Ast abgeht. Die Nerven für den M. add. posterior treten von rostro-lateral in den Muskel ein.

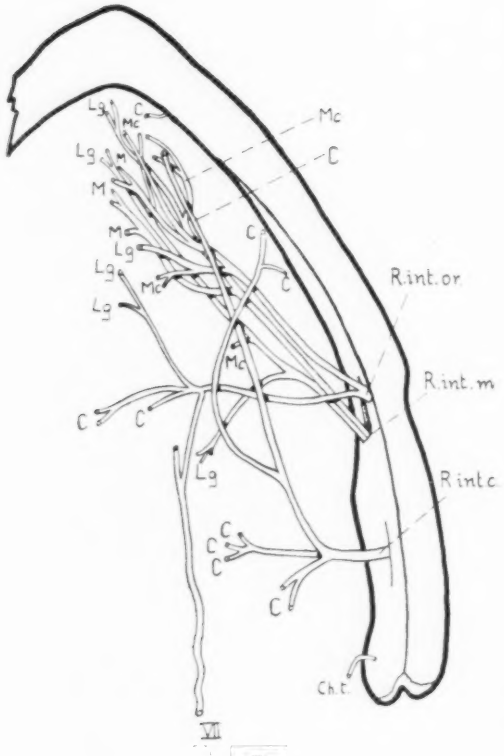
Nn. ad m. add. int: Die, entsprechend der Ausbildung der beiden Muskelportionen, zarten Nervchen entspringen stets medial vom R. mandibularis. Die Nn. pseudotemporales und pterygoidei besitzen einen gemeinsamen Ursprung am $R.V_3$ bei *Testudo, Pseudemys, Chrysemys, Amyda, Chelydra, Kinosternon, Sternotherus, Batrachemys* und getrennte Ursprünge bei *Dermochelys, Caretta, Malaclemys, Emys, Cuora, Terrapene* und *Pelusios*. Die P. pseudotemporalis wird durch 2 besonders zarte, mit gemeinsamer Wurzel proximal vom $R.V_3$ abgehende Ästchen (bei *Chelodina* und *Emys* entspringen diese Nervchen getrennt), die P. pterygoidea durch einen etwas kräftigeren Ast versorgt. Wenn die Nn.pseud. und der N.pter. getrennt entspringen, so ist der N.pter. stets der weiter distal vom $R.V_3$ abgehende Zweig. Bei den drei untersuchten Exemplaren von *Chelodina* entspringt ein Pseudotemporalisästchen lateral vom Ggl., das zweite entspringt aus gemeinsamer Wurzel mit zwei Nn. pterygoidei medial vom Ganglion. Bei *Emys* entspringt eines der beiden Pseudotemporalisästchen medial vom N. ad ang.oris (der in diesem Fall eine Strecke motorische Fasern mitführt), bald nach dessen Ursprung vom $R.V_3$, das zweite Ästchen etwas weiter ventral, medial vom $R.V_3$. Bei *Caretta* entspringt das eine der beiden Ästchen für die P. pseudotemporalis nicht vom $N.V_3$, sondern weit distal vom N. pterygoideus, der hier besonders kräftig ist. Bei *Kinosternon, Sternotherus, Pseudemys, Chrysemys, Batrachemys* und *Amyda* wird die P. pseudotemporalis nur durch einen einzigen, sich reich verzweigenden Ast versorgt. Die Nn. pseudotemporales dringen, nach kurzem Verlauf nach rostral, von caudal in den Muskel ein, wo sie sich zu dessen Versorgung entsprechend verästeln. Bei *Pseudemys* und *Testudo*, bei denen zwei Pseudotemporalisportionen auftreten, versorgt bei *Testudo* einer der beiden Äste die laterale, der andere die mediale

Partie; bei *Pseudemys*, bei welcher nur ein N. pseudotemporalis vorhanden ist, innerviert ein Seitenast von diesem die laterale Partie. Der N. pterygoideus, der oft beträchtlich weit distal der Nn. pseud. entspringt (*Dermochelys, Malaclemys, Emys, Terrapene*), zieht, medial des Add. externus, caudo-ventrad und tritt von caudo-dorsal in die P. pterygoidea ein.

Erst nach Eintritt des R. mandibularis in den Unterkiefer, wo er zum R. alveolaris wird, ergeben sich grössere Regelmässigkeiten im Nervenbild,



A



B

VOL 34 195

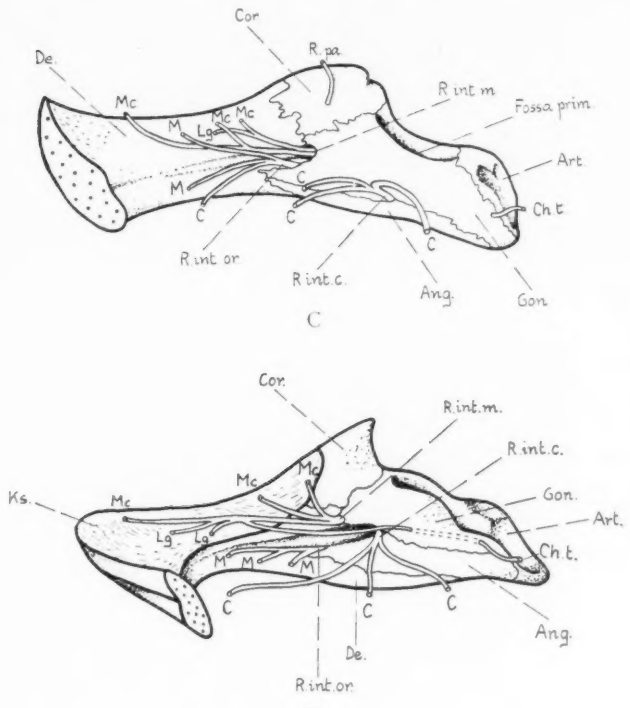


Abb. 10. Unterkiefernerven.
A *Dermochelys coriacea*. B *Chelydra serpentina*. C *Emys orbicularis*. D *Amyda sinensis*. Beachte den atypischen Verlauf der Chorda tympani.

obwohl auch hier eine bedeutende Variationsbreite vorliegt (Abb. 10). Der R. alveolaris gibt auf seinem Weg regelmässig zwei schwächere Äste ab, die zur Haut an der Aussenseite der Mandibel ziehen, weiters spaltet er drei kräftige Nerven zur Versorgung der Haut ventral des intermandibularen Muskels, der Zunge und Mundschleimhaut und des M.C_1v ab. Manchmal geht vom R. alveolaris (*Emys, Testudo, Malaclemys*), selten vom R. intermand. medius (*Caretta, Pseudemys*), ein zartes Nervchen ab, das ich Ramus paralingualis (N. lingualis posterior-FUCHS) nannte, welches durch ein eigenes Foramen im Coronoid die Mandibel medial verlässt und die Mundschleimhaut neben der Zunge versorgt. Schliesslich verzweigt sich der R.V_3 mehrfach im Gebiet der Unterkieferspitze. Diese Ästchen treten durch mehrere kleine Foramina (Foramina dentofacialia-GAUPP, FUCHS) lateral aus der Mandibel und versorgen die Hornscheide des Kiefers. Als Besonderheit sei erwähnt, dass sich bei *Cuora* der R. alveolaris, nach frühzeitiger Abgabe der Rr. intermand. caud., med. und or., gabelt und nun beide Äste im Canalis primordialis rostrad laufen und so

zwei Rami alveolares darstellen. Auf die genaueren Einzelheiten bezüglich der Nervenabgänge vom Ramus alveolaris will ich im Folgenden eingehen.

Kurz vor Eintritt in die Fossa prim. (*Chelydra, Pseudemys, Chrysemys, Malaclemys, Terrapene* und *Testudo*), oder erst innerhalb der Fossa (*Caretta, Dermochelys, Kinosternon, Sternotherus, Emys, Cuora, Chelodina, Bartachemys, Pelusios*) spaltet sich ventral bis ventro-lateral vom $R.V_3$ ein Ast — R. cutaneus recurrens der Autoren (Nervus cutaneus-LAKJER, N. auriculo-temporalis-FUCHS) — ab, nur bei *Pelusios* und *Kinosternon* sind es zwei Äste, die durch ein, bzw. mehrere Foramina im Supraangulare lateral die Mandibel verlassen und die Haut in der Gelenksregion und in der Gegend des Tympanon versorgen. Der R.cut.rec. kann auch vom R. intermand. caudalis abgehen (*Dermochelys, Clemmys, Testudo, Batrachemys, Pelusios, Amyda*), oder aus gemeinsamer Wurzel mit diesem vom $R.V_3$ entspringen (*Malaclemys*). In seinem Verlauf in der Mandibel gibt $R.V_3$ stets drei kräftigere Nervenäste ab. Bei *Pelusios* sind die beiden vorderen Äste sogar stärker als der R. alveolaris selbst. Der caudalst entspringende Ast — R. intermandibularis caudalis (N. mylohyoideus posterior-FUCHS, R. mylohyoideus-HOFFMANN) — zieht durch ein Foramen zwischen Angulare und Goniale nach medial und versorgt die Haut im Gebiet zwischen den Unterkieferästen. Bei *Chelodina* und *Cuora* versorgt dieser Nerv, abgesehen von der Haut, durch Abgabe eines Ästchens die Mundschleimhaut, bei *Pelusios* Haut, Mundschleimhaut und teilweise auch den $M.C_1v$. Der weiter rostral die Mandibel verlassende Ast — R. intermandibularis medius (N. lingualis anterior-FUCHS) — versorgt Zunge, Mundschleimhaut und die winzigen Sublingualdrüsen. Bei *Chelydra, Batrachemys* und *Pelusios* versorgt er zusätzlich einen Teil des $M.C_1v$, bei *Caretta* und *Chelodina* Zunge, Mundschleimhaut und den ganzen $M.C_1v$. Der rostralst austretende Nerv — R. intermandibularis oralis (N. mylohyoideus anterior-FUCHS) — innerviert den M. intermandibularis oralis ($M.C_1v$). Bei *Chelydra* versorgt er ausserdem die Haut, Zunge und Mundschleimhaut und geht eine Verbindung mit dem oberflächlich caudo-dorsal laufenden Facialisast, dessen genaue Herkunft ich nicht festgestellt habe, ein. Bei *Pelusios* versorgt dieser Ast nur Haut, Zunge und Mundschleimhaut, nicht aber den Muskel. Bei *Dermochelys* innerviert er, abgesehen vom Muskel, noch die Zunge, bei *Emys* Muskel und Haut, bei *Batrachemys* Muskel, Mundschleimhaut und Zunge und bei *Chelodina* und *Caretta* nur Mundschleimhaut und Zunge; bei letzterer stellt dieser Ast eine Querverbindung zu dem den Muskel versorgenden Ästchen des R. intermand. medius her. R. intermand. caud. und R. intermand. or. entspringen ventral bis lateral vom R. alveolaris, ziehen rostroventrad, lateral am MECKEL'schen Knorpel vorbei, biegen unter diesem nach medial um und treten durch die entsprechenden Foramina in, der Medialfläche der Mandibel, in das Gebiet zwischen den Unterkieferästen aus. Bei *Kinosternon scorpioides, Batrachemys, Clemmys* und *Terrapene* entspringt der R.

intermand. or. medio-ventral vom $R.V_3$; bei den beiden untersuchten Exemplaren von *Chelydra* fand ich den R. intermand. caud. und R. intermand. or. einmal mit gemeinsamer Wurzel, das andere Mal getrennt vom $R.V_3$ entspringend. Bei einem Exemplar von *Caretta,* bei *Dermochelys* und *Testudo* laufen der R. intermand. or. und der R. intermand. caud. eine grössere Strecke als einheitlicher Nerv, der sich erst relativ spät in die beiden Äste gabelt. Der R. intermand. medius entspringt immer medial vom $R.V_3$, zieht, dorsal vom MECKEL'schen Knorpel, rostrad und tritt zwischen R. intermand. or. und R. intermand. caud. nach medial aus. Mit dem R. intermandibularis medius verbindet sich die Chorda tympani, ein Facialisast, der bei allen Cheloniern durch ein Foramen im caudalsten Teil (Gelenksseite) des Goniale in die Mandibel eindringt, im Can.prim. eine kurze Strecke rostrad zieht und schliesslich medial in den R. intermand. medius mündet. Bei zwei der untersuchten Tiere (*Testudo* und *Amyda*) ist der Verlauf der Chorda tympani etwas abweichend. Bei diesen Tieren sieht man deutlich, dass es zu einem Grossteil die Facialisfasern sind, welche die Innervierung der Zunge besorgen. Bei *Testudo graeca* und *Amyda sinensis* tritt nun die Chorda wohl durch das entsprechende Foramen in die Mandibel, verlässt diese aber schon nach kurzem Verlauf durch ein, etwas weiter rostral, noch im Goniale befindliches Loch und zieht von dort an, medial der Mandibel, rostrad und verbindet sich endlich mit dem R. intermand. med.; von diesem, mit dem sie nicht so eng wie sonst verschmilzt, löst sie die Masse ihrer Fasern gleich wieder und innerviert als reines Facialiselement die Zunge. Da die Ausdehnung der den Unterkiefer zusammensetzenden Deckknochen sehr verschieden ist, kann auch über die Lage der Foramina für den R. intermand. medius und den R. intermand. oralis nur Allgemeines gesagt werden. R. intermand. med. verlässt stets gemeinsam mit dem MECKEL'schen Knorpel, diesem dorsal anliegend, R. intermand. or. nur wenig weiter rostral, ventral vom Knorpel, die Mandibel.

Nn. ad m. intra.: Bei *Pseudemys* und *Chrysemys* entspringt je 1 zartes Ästchen zur Versorgung dieses Muskels vom R. intermandibularis caudalis, in dessen proximalem Bereich. Bei *Caretta* entspringen 2 Nerven mit gemeinsamer Wurzel, bei einem zweiten Exemplar weit getrennt, medial vom R. intermand. caudalis.

Der Ramus alveolaris gibt dorsal einen schwächeren Ast ab — R. cutaneus externus der Autoren (N. cutaneus recurrens nervi alveolaris inferioris-FUCHS) — der durch ein auffallend grosses Foramen im Dentale (For. dentofaciale majus-FUCHS), oder durch mehrere kleine Foramina lateral austritt und die Haut versorgt. Bei *Testudo* entspringt der R.cut.ext. vom R. intermand. medius.

Eine bedeutende Rolle im Gebiet zwischen den Unterkieferästen spielt auch der N. facialis, der mittels der Chorda tympani die Zunge sensibel versorgt, weiters den M. intermandibularis caudalis ($M.C_2v$) und durch einen jederseits

VOL. 34 1953

weit nach rostral ziehenden Ast die Haut innerviert, aber auch oft ein Ästchen mit einem der drei Intermandibularisäste (jedoch nur Hautast) anastomosieren lässt und dadurch Facialisfasern mit denen des Trigeminus verbindet.

VERGLEICHENDER TEIL.

I. MUSKELN.

Während innerhalb der Ordnung der Crocodilier fast völlige Übereinstimmung in der Ausbildung der einzelnen Muskelpartien herrscht, tritt die Muskulatur bei den Cheloniern und Lacertiliern verhältnismässig stark differenziert auf, doch treten auch bei diesen grössere Abweichungen von dem bereits im beschreibenden Teil gebrachten Schema nur bei den Arten *Clemmys caspica* und *Cuora amboinensis* und der Lacertiliergattung *Uromastix* auf. Wohl eine der interessantesten, phylogenetisch noch nicht endgültig geklärten Erscheinungen ist die Ausbildung eines M. intramandibularis bei *Caretta* und den sog. „Schmuckschildkröten", wie *Pseudemys, Chrysemys* und *Graptemys*. Bei allen übrigen untersuchten Arten bleibt die Zahl der Muskelportionen konstant, wenn auch manigfaltige Variationen in Bezug auf Grösse, sehnige Differenzierungen und Verschiedenheiten in Ursprung und Ansatz auftreten. Bei der Familie der *Kinosternidae*, deren Arten sich bauplanmässig und in der Lebensweise nicht unterscheiden, treten auch in der Muskulatur nur geringfügige Unterschiede auf. Die sehr artenreiche Familie der *Testudinidae*, deren Vertreter sowohl geographisch weit getrennte Lebensräume bevölkern, als auch durch verschiedene Lebensweise auffallen, gehören doch dieser Familie rein aquatile, palustrische und extreme Landformen an, zeigt auch verschiedenen Schädelbau und reiche Differenzierungen der Muskulatur. Dagegen scheint, wie ich aus dem Vergleich mit LAKJER's Arbeit, der andere Arten untersuchte, ersah, bei den Familien der *Cheloniidae*, und *Trionychidae*, noch mehr als bei den *Kinosternidae*, die Muskulatur innerhalb der einzelnen Familien fast völlig übereinzustimmen. Zusammenfassend muss jedoch gesagt werden, dass die Verschiedenheiten, die innerhalb einzelner Familien auftreten, oft ebenso zahlreich sind wie die zwischen den einzelnen Familien, so dass ein Vergleich der Familien untereinander nicht gut möglich ist.

a) M. constrictor I dorsalis: Eine C_1d — Anlage konnte ich bei keiner der untersuchten Schildkröten feststellen; weder bei *Dermochelys*, bei der LAKJER (1926, P. 25) den Rest des M. levator bulbi und zwar dessen Pars dorsalis und ventralis feststellte, noch bei *Trionyx*, bei der LUBOSCH (1933, P. 642) ein zartes Bündelchen der Pars ventralis auf der rechten Seite eines Kopfes herauspräparierte. Doch muss hinzugefügt werden, dass mir von beiden Spezies nur je 1 Exemplar zur Verfügung stand, beides sehr junge

Tiere; der Kopf von *Dermochelys* hatte eine Länge von nur 5 cm, ein Umstand, der den Einwand LAKJER's, NICK habe den Lev. bulbi deshalb nicht gesehen, weil das ältere Tier diesen Muskel, vielleicht infolge postembryonaler Degeneration, nicht mehr besessen habe, entkräftet. Die von mir untersuchte Weichschildkröte gehört der Gattung *Amyda (Trionyx) sinensis* an, während LUBOSCH *Trionyx ferox* präparierte. HOFFMANN's Meinung (1896) in dem M. depressor palpebrae inferioris einen Rest der Constrictoranlage bei den Schildkröten identifiziert zu haben, wurde bereits von LAKJER als Trugschluss erklärt (P. 25 f.), da es sich hier um die kräftig ausgebildete glatte Lidmuskulatur handelt. FUCHS (1915, P. 122) wies, erstmals bei den Schildkröten, an Embryonen von *Emys* Reste der Schädelpterygoidmuskulatur nach. Auch nach EDGEWORTH (1935, P. 58) ist die C_1d-Muskulatur der Schildkröten wohl als Embryonalanlage vorhanden, atrophiert aber postembryonal. Nur *Dermochelys* soll postembryonal einen Protractor pterygoidei-Rest in Form einer zarten Fascie besitzen. Auch den Crocodiliern sprach EDGEWORTH embryonal die vollständige C_1d-Anlage (Lev. bulbi, Protractor und Levator pterygoidei) zu. Während sich die hintere Anlage gänzlich zurückbildet, bleibt die vordere als Levator bulbi, bzw. dessen Pars dorsalis auch beim adulten Tier erhalten. *Hatteria* und die Lacertilier besitzen die C_1d-Gruppe auch adult.

b) M. adductor mdb. externus: Eine bei den Schildkröten erstmalige Sonderdifferenzierung der P. superficialis, in der ich ein Homologon des M. anguli oris der Lacertilier und *Hatteria* sehe, fand ich bei *Terrapene, Pelusios* und *Chelodina*. Wie schon im beschreibenden Kapitel ausgeführt, zeigen *Terrapene* und *Pelusios* keine Abgrenzung der „M. ang. oris-Fasern" gegen die anderen Superficialisfasern. Bei *Terrapene* setzen sie am rostralen Teil des Buges der „Mundplatte", bei *Pelusios* an deren gesamten Bug an. Bei *Chelodina* hingegen erkennt man ein stärkeres, rostrales, von der Masse der Superficialisfasern deutlich getrenntes Muskelbündel, welches am Rostralabschnitt des Buges der „Mundplatte" inseriert. Die Innervierung dieses Superficialisteiles wird durch ein, von dem diese Portion versorgenden Nerv abgehendes Ästchen durchgeführt. Auch bei den Eidechsen sind mehrere Möglichkeiten der Ausbildung eines M. anguli oris gegeben. Bei *Tupinambis teguixin* und *Lacerta ocellata* setzt dieser, vom übrigen Superficialis gut abgrenzbare Muskel am Rostralabschnitt des Buges der „Mundplatte" (Vgl. *Chelodina*), beim Grossteil der anderen Lacertilier am gesamten Bug an. Bei *Tarentola mauritanica* ist der, am gesamten Bug ansetzende Muskel gegen die Fasern des Superficialis fast nicht abgrenzbar (Vgl. *Pelusios*). Die Innervation entspricht der bei den Schildkröten beobachteten. Diese und weitere Befunde über die Lacertilier und *Hatteria* entnahm ich den Arbeiten von POGLAYEN Ingeborg (1953). Bisher wurde in der Literatur von einer dem M. anguli oris ähnelnden Bildung bei Schildkröten nichts erwähnt; auch LAKJER, der eine *Terrapene* nahe verwandte Art untersuchte, machte diesbezüglich keine

VOL. 34 1953

Mitteilungen. Zur Ausbildung der kräftigen, den Externusportionen zum Ansatz dienenden Binnensehne, welche den Schildkröten, *Hatteria* und den Lacertiliern, nicht aber den Krokodilen zukommt, sei noch gesagt, dass diese, wie schon LAKJER bemerkte, nur bei *Dermochelys* in Reduktion begriffen ist. Die Ausbildung einer Sehnentasche bei *Chelone*, in der ein Teil der Fasern der P. profunda inseriert, dürfte LAKJER übersehen haben, da er einen Teil der Fasern am oberen und mittleren Abschnitt der Medialfläche der Binnensehne, einen anderen Teil (rostrale Fasern) am Coronoid und Supraangulare ansetzen liess (LAKJER, P. 51). Angesichts der Tatsache, dass im Schädelbau keine, die Ausbildung der Muskulatur beeinflussenden Verschiedenheiten bestehen und LAKJER's Befunde mit den meinen weitgehend übereinstimmen, obwohl es sich hier um zwei verschiedene Gattungen handelt — *Caretta caretta* und *Chelone imbricata* — habe ich keine Bedenken LAKJER's Ergebnisse zum Vergleich heranzuziehen.

Im Ansatzgebiet der ventro-rostralen Fasern der P. media ergeben sich insofern mit LAKJER's Befunden (P. 50 f.) Verschiedenheiten, als er diese nur an der Medialfläche des Supraangulare und nicht, wie es nach meinen Befunden meist der Fall ist, auch am Rostro-Ventralabschnitt der Binnensehne ansetzen sah. Im besonderen Widerspruch zu meinen Untersuchungsergebnissen an *Dermochelys* steht LAKJER's Befund, nach welchem, wegen der starken Rückbildung der Binnensehne, keine Mediusfasern an dieser inserieren. Ich fand den Ansatz dieser Fasern bei *Dermochelys* zum Grossteil an der Binnensehne und nur zum geringen Teil an der Caudo-Medialfläche des Supraangulare. Bei *Amyda sinensis* stimmen meine Befunde mit den von LAKJER über *Trionyx cartilagineus* erhobenen, bis auf die von diesem Autor festgestellte Dreiteilung der P. media, überein. Die P. media ist bei *Amyda* einheitlich, doch ist es möglich, dass dieser Zustand eine artbedingte Variation darstellt. Auch die P. profunda, die den grössten Teil der Binnensehne als Ansatzgebiet benützt, inseriert bei Dermochelys nach LAKJER direkt, sehnig am Dentale. Diese kleine Ansatzsehne vertritt hier, nach LAKJER, die Binnensehne (P. 51 f.). Die Tatsache, dass eine kleine, rostro-medial der P. profunda typica gelegene und dorso-lateral der P. pseudotemporalis entspringende, zur Gänze bei *Clemmys* und teilweise bei *Cuora* (zahlreiche Fasern strahlen bei *Cuora* in die Gaumenhaut ein) an der Binnensehne des Add. externus ansetzt, bewogen mich diese Partie als P. profunda atypica zu bezeichnen. Diese wird auch durch ein Externusästchen innerviert. Die bei *Cuora* an der Gaumenhaut inserierenden Fasern bewirken bei ihrer Kontraktion eine Erweiterung der Mundhöhle.

Die drei Muskelpartien des Add. externus sind bei den Cheloniern und Lacertiliern immer gut abgrenzbar, nur bei *Tupinambis* und *Tarentola* sind die einzelnen Portionen nicht zu unterscheiden. Bei den Crocodiliern geht die P. media im Ursprungsgebiet in die P. superficialis, im An-

satzgebiet in den Add. posterior über; auch fehlt diesen die gemeinsame Sehnenbildung (Binnensehne).

c) M. adductor mdb. p o s t e r i o r: LUTHER (1914, P. 117) bezeichnete den primären Adductor der Vertebraten, wegen seiner Lage caudal vom R.V_3, als Add. posterior, aus dem durch dorso-laterale und rostrale Differenzierung der Add. externus und internus entstanden. Der Adductor posterior der Amphibien und Sauropsiden wäre also dem Rest des „Ur-Posterior" gleichzusetzen. Er tritt durch die Reihe der Sauropsiden als einheitlicher Muskel auf, doch ist er nicht immer sehr deutlich vom Add. externus oder internus abgrenzbar. Der Muskel weist oft Doppelinnervation auf (LUTHER, LUBOSCH, HOFER).

Bei den Cheloniern, den Lacertiliern und *Hatteria* ist er von den anderen Adductoren gut unterscheidbar, bei den Crocodiliern hingegen weist er einen Übergang zur P. media des Add. ext. und zu den oberflächlichen Fasern des M. pter. posterior in dessen Ursprungsgebiet auf. Auf Grund der Innervierung steht der Add. posterior bei den Cheloniern, Lacertiliern (Ausnahme *Chamaeleo*) und *Hatteria* mit dem Add. externus, bei den Crocodiliern und *Chamaeleo* mit dem Add. internus in Beziehung. Bei ersteren entspringt meist ein Posteriornerv vom N. externus, bei letzteren gehen die den Add.post. versorgenden Aestchen stets vom N.pter.post.bzw. N.pter.ab. Der Befund bei Krokodilen weist, was dieses Merkmal betrifft, auf eine engere Verwandtschaft zu den Vögeln hin. Bei den Vögeln entspringen die Nn.post. stets vom auffallend kräftigen N. pterygoideus, manchmal entspringt zusätzlich noch ein Aestchen direkt caudal vom R.V_3 (HOFER 1950, P. 495, 507, f.); bei den Krokodilen gehen die Nn.post. immer vom N. pterygoideus ab, der bei diesen nicht ganz so stark ist wie bei den Vögeln.

LUBOSCH (1933, P. 654, 1938, P. 1036, ff.) warf die Frage auf, ob „der Adductor posterior wirklich ein den beiden anderen Muskeln gleichgeordneter dritter Muskel, dessen Bestimmung es daneben ist den beiden anderen Zuwachs zu gewähren" sei, oder der Add. externus und Add. internus sich von dem primären Add. posterior „der Fläche nach zu grösserer Selbständigkeit sonderten", also sagen wir mobil werdende Teile des Add. posterior sind, die später, besonders bei den Sauropsiden, eine reiche Differenzierung erfahren. Am wahrscheinlichsten halte ich eine Synthese der Meinungen LUTHER's und LUBOSCH's, indem die Adductormuskulatur ursprünglich einheitlich war („Ur-Posterior" LUTHER's) und sich Add.ext. und int. erst später der Fläche nach allmählich sonderten, aber auch nebenbei Nachschub von Posteriormaterial erhalten haben dürften. Die Doppelinnervation des Adductor posterior beweist wohl seine „Doppelnatur" wie LUBOSCH sagte, d.h. seine Bindungen mit den anderen Adductoren, nicht jedoch die absolute Richtigkeit seines oder LUTHER's Standpunktes in der Frage der Entstehung von Add.ext. und int.

Mein Befund bei *Dermochelys* widerlegt die Annahme LAKJER's, der bei

diesem Tier eine Trennung des Add.post. in eine rostrale und eine caudale Portion beobachtete.

d) M. adductor mdb. internus: Dieser Muskelkomplex ist bei den Schildkröten, Krokodilen, Eidechsen und *Hatteria* sehr verschieden gestaltet. Bei den Krokodilen treten drei selbständige Partien auf, von denen der M.pter. anterior und der M. pseudotemporalis innervationsmässig zusammenhängen; bei *Hatteria* finden sich eine P. pter. anterior und eine P. pter. posterior vor, die innervationsmässig miteinander in Beziehung stehen. Ähnlichkeit zu den Lacertiliern weist *Hatteria* durch die Ausbildung zweier Pseudotemporalisportionen (Pseudotemporalis superficialis und profundus) auf. Die Schildkröten besitzen nur zwei eng zusammenhängende Internusportionen (gemeinsamer Ansatz, Nerven entspringen aus gemeinsamer Wurzel, medial vom R.V_3). Bei den Eidechsen besteht weder in der Innervation, noch in Ursprung oder Ansatz eine engere Beziehung zwischen Pseudotemporalis und Pterygoideus, wenn man von der allgemeinen Charakterisierung dieser Muskeln als Internusbestandteile, durch den medialen Ursprung ihrer Nerven vom R.V_3 absieht. LAKJER (p. 69) behauptete, dass bei den Schildkröten, ausgenommen *Trionyx*, eine völlige Trennung zwischen dem Add.int. pseudotemporalis und pterygoideus vorliege. Ich kann mich dieser Meinung nicht anschliessen, da diese Internusteile bei allen untersuchten Tieren, mit Ausnahme von *Caretta* und *Dermochelys*, nicht als selbständige Muskeln auftreten, sondern eine gemeinsame Sehne besitzen, mit Hilfe derer sie an der Mandibel inserieren. Es wurde daher der Add. internus in eine Portio pseudotemporalis und eine Portio pterygoidea und nicht, wie von LAKJER (1926) und LUBOSCH (1933), einen Musculus pseudotemporalis und einen Musculus pterygoideus eingeteilt. Die Innervation zeigt, dass die beiden Portionen entweder von zwei aus gemeinsamer Wurzel oder getrennt vom R.V_3 medial entspringenden Aesten versorgt werden. LUBOSCH nahm (1938, P. 1034, f.) bei Besprechung des Add. internus nicht näher Stellung zu der engen Zusammengehörigkeit der beiden Internusportionen bei Cheloniern. Bei *Pseudemys* erfolgt eine Teilung des Pseudotemporalis in eine laterale und mediale Partie, die beide dem Adductor internus angehören, da sie ein gemeinsames, für die P. pseudotemporalis charakteristisches Ursprungsgebiet besitzen, auch im Ansatz in keine Beziehung zum Add. externus, resp. dessen Binnensehne treten und beide Partien vom N. pseudotemporalis versorgt werden. Der bei *Testudo* zweiköpfig entspringende Muskel gehört in seiner Gesamtheit dem Pseudotemporalis an, da er 1. den Raum einnimmt, der diesem Muskel zukommt, 2. die bekannte, gemeinsame Aponeurose mit der P. pterygoidea besitzt und 3. auch durch die Innervation als Pseudotemporalis erkenntlich ist. Interessant ist die Tatsache, dass bei den Eidechsen, Vögeln und *Hatteria* (nicht bei den Krokodilen und Schildkröten) der Pseudotemporalis regelmässig zweiteilig, als P. superficialis und P. profunda auftritt. Allerdings steht nicht mit Sicherheit fest, ob bei den

VOL. 34 1953

Vögeln der Pseudotemporalis profundus der Autoren (M. quadrato-mandibularis nach HOFER 1950) den tieferen Portionen des Pseudotemporalis mancher Reptilordnungen homolog ist, oder ob er als Abspaltung des M. pterygoideus oder des Add. posterior der Vögel betrachtet werden muss (HOFER 1950, P. 478). Es verdient hervorgehoben zu werden, dass bei *Caretta,* als einziger Schildkröte, die Ursprünge der P. pseudotemporalis und P. pterygoidea weit nach rostral an das Interorbitalseptum und bis zum Palatinum vorgeschoben sind, so dass der Muskel in seiner Gesamtheit der P. pterygoidea anterior (M. pterygoideus atypicus — nach Ingeborg POGLAYEN, 1953) von *Hatteria* sehr ähnlich sieht. Bei *Chelone* liess LAKJER, in Unkenntnis der Existenz des M. intramandibularis, die P. pseudotemporalis an der Sehne der P. pterygoidea und somit gemeinsam mit dieser am Goniale inserieren. Richtig ist, dass die P.pter. selbständig am Goniale inseriert, während die P.pseud. in eine Sehne übergeht, die in die Fossa prim. zieht und sich teilweise zum M. intra. auffasert, der am Boden der Fossa ansetzt. Bei *Chelodina,* bei welcher die Sehne der P. pseudotemporalis und einige deren mediale Muskelfasern selbständig, dorsal am MECKEL'schen Knorpel, also in der Fossa prim. inserieren, ist wohl zu beachten, dass es sich hier nicht etwa um einen M.intra., dessen Fasern in die Fossa laufen, sondern um echte Pseudotemporalisfasern handelt.

e) Der M. intramandibularis: stellt eine selbständige Adductorpartie dar, da er, von der Voraussetzung LUTHER's ausgehend, phylogenetisch den anderen Adductoren gleichgestellt ist und eine selbständige Innervierung durch vom R. alveolaris abgehende Aeste aufweist (vgl. Ivo POGLAYEN 1953). Bei den Schildkröten tritt der Muskel durch seine Lage speziell zur P. pseudotemporalis des Add.int. in engere Beziehung, er behält aber seine selbständige nervöse Versorgung stets bei. Er ist hier nicht so kräftig und reicht im Canalis primordialis nicht so weit rostrad wie bei *Alligator.* Eine spezielle funktionelle Bedeutung dieses Muskels ist bei den Cheloniern schwer ersichtlich.

f) M. intermandibularis: Bei den *Selachii* und *Chondrostei* (*Polyodon*) ist der Muskel einheitlich und in seiner Gesamtheit vom N.V versorgt, bei *Acipenser* ein wohl zusammenhängender, aber in verschiedene Portionen gegliederter Muskel. Bei den *Holostei* (*Amia*) kommt es zur Teilung in eine orale und caudale Partie, die vom N.V. bzw. N.VII versorgt wird (LUTHER, 1909, 1913). Der Muskel ist auch bei den Amphibien in zwei Partien differenziert, die beide vom N.V innerviert werden. Dieser Ansicht sind GAUPP (1896), DRÜNER (1901) und LUTHER (1914). 1864 warf FISCHER die Frage einer eventuellen Innervierung auch durch Facialisfasern auf. VETTER und RUGE nahmen noch an, dass der intermandibulare Muskel der Selachier ausschliesslich vom N.VII versorgt werde. Es gibt jedoch schon bei den Selachiern einen $M.C_{IV}$, dessen Existenz ALLIS (1897), K. FÜRBRINGER (1902), DRÜNER (1903) und LUTHER (1909) nachwiesen. RUGE vertrat die Meinung, dass der gesamte

intermandibulare Muskel bei den Reptilien vom N.VII innerviert würde. Die Pars oralis des M. intermandibularis ist nur bei den Anuren gut ausgebildet, bei adulten Urodelen fehlt sie mit Ausnahme von *Salamandra* (WALTERS 1887), während sie larval bei diesen immer vorhanden ist. Ihr Fehlen ist daher sekundär. Bei Gymnophionen ist die Pars oralis reduziert (LUTHER 1914).

Der M. intermandibularis tritt bei den Sauropsiden teils einheitlich, teils gegliedert (manche Lacertilier) auf. Während der rostrale Teil stets vom N.V versorgt wird, innerviert den caudalen Teil des M. intermandibularis der N.VII. Der M. intermandibularis zeigt bei den Cheloniern und Lacertiliern in seiner Ausbildung grosse Variabilität, wogegen er bei den Crocodiliern immer in gleichbleibender Form auftritt. *Hatteria* gleicht in der Ausbildung des Muskels völlig den Crocodiliern. Der rostrale Teil — Pars oralis ($M.C_1v$) — wird vom N. trigeminus innerviert, während der hintere Teil — Pars caudalis ($M.C_2v$) — der caudal an den M. sphincter colli grenzt, vom N. facialis versorgt wird. Es bestehen bei den Cheloniern wohl Anastomosenbildungen zwischen N.V und N.VII, doch nur zwischen Aestchen, die die Haut versorgen und zu dem Muskel in keiner Beziehung stehen. Bei den Crocodiliern besteht im caudalen Gebiet der Pars oralis und im rostralen Gebiet der Pars caudalis ein fliessender Übergang auch in der Innervierung, da die Pars caudalis in ihrem vorderen Abschnitt, neben der Versorgung durch den N.VII, auch durch ein Aestchen des N.V innerviert wird. Über RUGES Meinung vgl. IVO POGLAYEN (1953).

VOL. 34 1953

II. NERVEN.

Von GAUPP, FUCHS, LUBOSCH und anderen Autoren wurde bereits eine detaillierte Analyse der Trigeminusverzweigungen, insbesondere im Bereiche des Unterkiefers, vorgenommen. Man konnte aber die Bedeutung der einzelnen Befunde noch nicht richtig bewerten, weil es an dem notwendigen breiten Material, das ähnlich genau untersucht hätte werden können, fehlte.

Das Verhalten der Nerven ist für jede Ordnung charakteristisch. Bereits in der Ausbildung des Ggl. trigemini finden wir grundlegende Unterschiede. Bei den Schildkröten sind Ggl. ophthalmicum und Ggl. maxillo-mandibulare weitgehend verschmolzen, bei Krokodilen, im Schnitt noch nachweisbar, getrennt, ein Zustand der nach FUCHS (1915, P. 106, f.) erstere in nähere Beziehung zum Säugetierzustand bringt, letztere als primitiver zu den Rhynchocephaliern, Sauriern und Schlangen stellt. Wesentliche Unterschiede bestehen auch in dem Vorhandensein eines $N.C_1d$ ($N.V_4$) bei allen übrigen Sauropsiden im Gegensatz zu den Cheloniern. Bei den Crocodiliern findet sich ein den M.pterygoideus anterior, den M. pseudotemporalis und einen Teil der P. profunda des Add.ext. versorgender gemeinsamer Nerv mit medialem Ursprung vom $R.V_3$; auch bei den meisten Lacertiliern entspringt ein N. pseudotempora-

lis lateral vom R.V_3 womit, das von LAKJER aufgestellte und von LUBOSCH bestätigte Schema, wonach bei den Reptilien die den Add. externus versorgenden Aeste alle lateral, die Nerven für den Add. internus medial, ohne Beziehung zu ersteren, vom Stamme des V_3 entspringen, durchbrochen wird. Ferner ist die Versorgung des Add. posterior bei Krokodilen und Vögeln einerseits und bei Cheloniern und Lacertiliern andererseits grundverschieden. Bei ersteren geht der N.add.post. stets von dem den M. pterygoideus posterior innervierenden Ast ab; bei den Vögeln entspringt zuweilen noch ein Aestchen caudal vom R. V_3. Bei den Lacertiliern entspringt der N.add.post. meist vom N. externus, bei wenigen Tieren tritt Doppelinnervation auf, indem noch ein zweites Aestchen caudo-lateral vom Stamme des V_3 abgeht. Nur bei *Chamaeleo* entspringt ein Ast vom R.V_3, ein zweiter vom N. pterygoideus. Eine Versorgung des Add.post. nur vom Stamme kommt ausschliesslich bei *Uromastix* vor. Bei den Cheloniern verhalten sich die Nn.add.post. gleichfalls sehr variabel. Entweder entspringt bei diesen 1 Ast selbständig vom R.V_3 und ein 2. Ast vom N. externus, oder ist nur einer der beiden Aeste ausgebildet. Nie kommt es aber bei Schildkröten, Eidechsen (Ausnahme *Chamaeleo*) und *Hatteria* zu einer Bindung des N.add.post. an den N. internus, wie dies für Krokodile und Vögel typisch ist. Ebenso wie bei den Cheloniern gibt auch bei den Sauriern, *Hatteria* und den Crocodiliern der R. alveolaris die 3 typischen Intermandibularisäste ab, mit dem Unterschied, dass bei den Crocodiliern jeder Ast konstant seine bestimmten Gewebe innerviert, während bei den Cheloniern und Sauriern sich die Aeste in der Wahl ihrer Versorgungsgebiete sehr variabel verhalten. Eine bedeutende Rolle im Gebiet zwischen den Unterkiefern spielt auch der N.VII, der nicht nur den M.C_2v und durch einen beiderseits weit nach rostral ziehenden Ast die Haut versorgt, sondern noch mit einem der drei Hauptäste (jedoch nur Hautast) des Trigeminus anastomosieren kann und dadurch Facialisfasern mit denen des Trigeminus verbindet. Eine Doppelinnervation des Muskels (M.C_2v) kommt nur bei Krokodilen vor. Die Chorda tympani des N. facialis verbindet sich bei den Schildkröten immer mit dem R. intermand. medius, mündet aber bei den Krokodilen stets und bei den Eidechsen meist in den R. alveolaris; nur selten mündet die Chorda bei letztgenannten in den R. intermand. oralis, bzw. medius.

LAKJER (1926) stellte folgendes grobe Nervenschema der Chelonier auf:

1—2 Nerven mit lateralem Ursprung vom R.V_3 . .	Add.mdb.externus
1 Nerv mit medialem Ursprung vom R.V_3	Add.post.+Add.int.pseud.+ Add.int.pter.

Für *Chelone imbricata* zusätzlich 2 Nn.add.post. mit medialem Ursprung vom R.V_3. LUBOSCH (1933) übernahm grundsätzlich dieses Schema und führte es speziell für *Chelone mydas* weiter aus. Er stellte fest:

1 Nerv mit latero-rostralem Ursprung vom $R.V_2$ .. Add.externus
1 Ast mit medialem Ursprung vom $R.V_3$ ..... Add.int.pter. + Add.post.
1 selbständig vom $R.V_3$ entspringender Ast ..... Add.post.
zahlreiche medial vom $R.V_3$ entspringende Zweige .. Add.int.pseud.

Zum Allgemeinschema habe ich Folgendes zu sagen: Ich fand stets 2 Nn.add.ext. mit lateralem Ursprung vom $R.V_3$, nur bei *Caretta* fand ich einen und bei *Batrachemys* und *Pelusios* deren drei. Zur Versorgung des Add.int. stellte ich immer zwei (1 N.pseud., 1 N.pter.) getrennt oder aus gemeinsamer Wurzel, medial vom $R.V_3$ abgehende Äste fest; bei *Caretta* erhält die P.pseud. zusätzlich ein zartes Aestchen vom N.pter. Der Add.post. erhält seine Nerven entweder vom Add.ext., oder caudo-medial vom Stamme des V_3, oder aus beiden Quellen. Nie treten jedoch die Nn.add.post, mit einem N. internus in Beziehung. Der Vergleich mit der Arbeit von Fuchs (1931) — Fuchs modellierte in vortrefflicher Weise Unterkiefer und Nervenverlauf von embryonalen Schädeln —, zeigt weitgehende Übereinstimmung mit meinem allgemeinen Nervenschema dieser Region. Die von mir beschriebenen Nervenäste des Unterkiefers entsprechen in Zahl und Ursprung den von Fuchs geschilderten. Im Verlauf ergeben sich kleinere Unterschiede, vielleicht zum Teil dadurch bedingt, dass meine Untersuchungen an voll entwickelten Tieren durchgeführt wurden, andererseits auch für diese von mir nicht untersuchte Gattung charakteristisch sein dürften. Die Angaben Fuchs' über die Versorgungsgebiete der einzelnen Unterkiefernerven dürfen nicht verallgemeinert werden; soweit die Angaben zutreffen, haben sie bei der grossen Variabilität im Chelonierstamme natürlich nur für diese eine Gattung Gültigkeit. Ich möchte mit dieser Aussage keinesfalls die gewissenhafte und auf diesem Gebiet erstmalige Arbeit von Fuchs angreifen, glaube aber, dass meine Stellungnahme, infolge der Erfahrung durch die Präparation so zahlreichen Materials, vertretbar ist.

Im Folgenden will ich näher auf Fuchs' Befunde bei *Podocnemis* eingehen und zeigen, inwieweit die Resultate mit meinem Allgemeinschema der Unterkiefernerven nicht übereinstimmen.

Fuchs fand bei seinen Embryonalserien den Canalis nervi alveolaris noch als Rinne — Sulcus alveolaris inferior (Fuchs) — vor; dieser schliesst sich also erst spät zum Canalis primordialis. Bei keiner der von mir untersuchten Schildkröten wurde eine Schlingenbildung eines mit zwei Wurzeln vom R. alveolaris entspringenden R. cutaneus recurrens festgestellt, doch wurde dieser Zustand auch von Fuchs nur bei einer Schnittserie beobachtet. Der Autor liess daher die Frage offen, ob der Nerv immer oder nur gelegentlich als Variation mit zwei Wurzeln am Hauptstamm entspringt. Dazu möchte ich sagen, dass ähnliche Variationen häufig vorkommen, jedoch ohne Schlingenbildung, d.h. dass sich die beiden Wurzeln nicht zu einem einheitlichen R.cut.rec. vereinigen.

VOL. 34 1953

(z.B. *Kinosternon leucostomum*, bei der 2 Rr.cut.rec. vom $R.V_3$ abgehen). Auch der direkte Ursprung am R. alveolaris ist nach meinen Befunden absolut nicht festgelegt, denn oft entspringt der R.cut.rec. vom R. intermand. caudalis. Der zarte Nervus cutaneus lateralis maxillae inferioris, den FUCHS beim *Podocnemis*embryo neben dem R.cut.rec. entspringen sah und der ebenfalls die Haut der Gelenksregion versorgt, gehört zweifellos, wie auch FUCHS vermutete, als zweite Wurzel zum R. cut. rec. Der N. mylohyoideus posterior (mein R. intermand. caudalis) versorgt nach FUCHS die hintere Partie des M. intermandibularis (P. caudalis), ein Befund, den ich sehr anzweifle, da ich bei keinem Tier eine Innervation des caudalen Teiles des M. intermandibularis durch Trigeminusäste, stets aber durch solche des Facialis nachweisen konnte. Eben erwähnter Ast versorgt bei der Mehrzahl der von mir untersuchten Tiere die Haut zwischen den Unterkieferästen; nur bei *Pelusios* versorgt er, abgesehen von der Haut, auch die Mundschleimhaut und den $M.C_1v$. FUCHS beschrieb überhaupt keinen die Haut dieser Region versorgenden Ast. Der N. mylohyoideus anterior (mein R. intermand. oralis) versorgt nach FUCHS den vorderen Teil des intermandibularen Muskels (P. oralis). Dies trifft auch für die überwiegende Zahl der von mir untersuchten Tiere zu. M. lingualis anterior (mein R. intermand. medius) und N. lingualis posterior (mein R. paralingualis) innervieren nach FUCHS nur die Zunge; sie entspringen bei *Podocnemis* als einheitlicher Nerv — N. lingualis (R. intermand. med.) — und gabeln sich erst nach Einmündung der Chorda tympani. Der R. paralingualis kann nach meinen Beobachtungen auch allein direkt vom R. alveolaris abgehen, kann aber auch gänzlich fehlen. Der R. intermand. med. versorgt nach meinen Befunden nicht nur die Zunge, sondern auch die Mundschleimhaut und kann sogar motorische Fasern mitführen, die den M. intermand. oralis ($M.C_1v$) versorgen (*Caretta, Chelodina, Chelydra, Batrachemys, Pelusios*). Die Chorda tympani fand FUCHS bei *Podocnemis* und *Emys*, nicht aber bei *Chelone imbricata* und *Chelone mydas*. Bei der nächstverwandten Form der beiden letztgenannten Arten, nämlich *Caretta caretta*, konnte ich die Chorda wie bei allen anderen Cheloniern in typischem Verlauf feststellen. Ich halte es daher für unwahrscheinlich, dass sie nur bei *Chelone* fehlen oder völlig anders laufen sollte.

Was die Versorgung des M. intramandibularis betrifft, wird dieser bei den Schildkröten stets durch 1 oder 2 zarte vom R. intermand. caudalis abgehende Aestchen, bei den Krokodilen durch mehrere, feine Nervchen, die direkt vom R. alveolaris entspringen, innerviert. Bei den Schildkröten tritt nicht nur zwischen den einzelnen Gattungen, sondern auch Arten, ja sogar an beiden Seiten des Kopfes eines Individuums mehr oder minder grosse Variabilität im Nervenbild auf. Freilich sind die Unterschiede an einem Tier oder zwischen Tieren verschiedener Arten nie so auffallend wie etwa zwischen Gattungen

und Familien. Trotz zahlreicher Verschiedenheiten bleibt der Cheloniercharakter des Nervenschemas stets gewahrt.

So konnte ich bei 2 Exemplaren von *Caretta caretta* folgende Unterschiede feststellen: Der R. intermand.caud und R. intermand.or. entspringen einmal getrennt, das andere Mal mit gemeinsamer Wurzel vom R. alveolaris, wobei sie sich erst spät trennen. Während bei dem einen Tier die beiden Nn.intra. getrennt vom R.intermand.caud. abgehen, entspringen sie bei dem anderen mit gemeinsamer Wurzel proximal vom R.intermand.caud. Beim ersten Tier zweigt von einem Aestchen des R.intermand.med. der R. paralingualis zur Mundschleimhaut ab, beim zweiten Tier geht vom Hauptast des R. intermand.med. ein Nervchen ab, das die Haut rostral vom Coronoid versorgt. Bei den Unterkiefernerven eines Individuums von *Chelydra* treten folgende Variationen auf: beim linken Unterkiefer fand ich getrennte Ursprünge für die Rr. intermand.caud. und intermand.or. und einen einheitlichen R. intermand.med. Am rechten Unterkiefer entspringen R.intermand.caud. und R.intermand.or. mit gemeinsamer Wurzel vom $R.V_3$, der R.intermand.med. spaltet sich noch innerhalb des Canalis prim. in zwei gleich starke Aeste, die, eng verbunden, im Gebiet zwischen den Unterkiefern weit nach rostral ziehen, bevor sie sich endgültig trennen. Bei *Kinosternon leucostomum* gabelt sich der $R.V_2$ viel weiter caudal als bei *K. scorpioides*, weiters entspringt der N.ad. ang.or. etwas weiter dorsal vom $R.V_3$ und treten bei *K. leucostomum* 2 Rr.cut.rec. statt 1 R.cut.rec. wie bei *K. scorpioides* auf. Der $R.V_2$ durchläuft auf der linken Seite eines Kopfes von *Cuora* die P. pseudotemporalis in deren ganzer Ausdehnung ohne lateral sichtbar zu werden. Auf der anderen Seite desselben Kopfes wird der $R.V_2$ nur von einem caudalen Faserbündel des Muskels lateral bedeckt und läuft sonst dem Muskel lateral anliegend.

ZUSAMMENFASSUNG.

In vorliegender Arbeit wurden die Kiefermuskulatur und die Verzweigungen des Nervus trigeminus der Schildkröten untersucht.

Erstmalig untersucht wurden die Genera *Batrachemys, Chelodina, Chrysemys, Pseudemys, Graptemys, Cuora, Malaclemys, Kinosternon, Sternotherus* und die Spezies *Clemmys guttata* und *Terrapene triunguis*.

Die Derivate des Constrictor I dorsalis (CId) fehlen bei allen untersuchten Cheloniern postembryonal.

Es wurde bei einem Vertreter der *Cheloniidae (Caretta caretta)* und bei drei Gattungen der *Testudinidae*, Unterfam. *Emydinae (Pseudemys scripta troostii, Chrysemys picta, Graptemys pseudogeographica)* erstmalig das Vorhandensein eines M. intramandibularis, mit von den anderen Adductormuskeln unabhängiger nervöser Versorgung nachgewiesen. Die zarten Nn. ad M. intramandi-

VOL. 34 1953

bularem gehen stets vom Ramus intermandibularis caudalis ab, der selbst vom Ramus alveolaris entspringt und die Haut zwischen den Unterkieferästen versorgt.

Für den stets vom N. trigeminus innervierten M. intermandibularis oralis ($M.C_1v$) wurden zwei verschiedene Ausbildungsmöglichkeiten festgestellt.

Die Untersuchungen zeigten, dass das von LAKJER für die Chelonier aufgestellte Innervationsschema nur zum Teil zutrifft, da nach meinen Befunden der N. ad Add. posteriorem niemals mit dem N. internus in Beziehung tritt. Vielmehr steht der Adductor posterior durch seine Innervation mit dem Adductor externus in Verbindung, da er meist durch einen vom N.add.ext. abgehenden, oft noch von einem zweiten, selbständig vom $R.V_3$ entspringenden und nur selten von einem einzigen, vom $R.V_3$ caudal bis caudo-medial abgehenden Nerv versorgt wird.

Durch meine Untersuchungen an 29 Cheloniern (20 Arten) bin ich nun in der Lage ein exaktes Nervenschema zu bringen.

Vom R. mandibularis gehen folgende Aeste ab:

2 Aeste zum Add. externus mit lateralem Ursprung vom $R.V_3$ (bei *Caretta* fand ich nur 1 N. add.ext., bei *Batrachemys* und *Pelusios* je 3 Nn.add.ext.).

2 medial, oft gemeinsam entspringende Aeste für den Add. internus (je 1 N. pseudotemporalis und N. pterygoideus).

1 caudal bis caudo-medial (nie gemeinsam mit dem N. internus) vom $R.V_3$ entspringender Ast zum Add. posterior, oder 1—2 vom N. externus abgehende Aeste zum Add.post., oder Doppelinnervation aus beiden Quellen.

1 rostral bis rostro-lateral vom $R.V_3$ abgehender sensibler N. ad angulum oris (nur bei *Dermochelys* entspringt dieser Nerv vom R. V_2).

Chelodina bildet unter den Schildkröten eine Ausnahme, indem bei diesem Tier 1 Externusast, alle Internusäste und der N. ad ang.or. vom Ganglion trigemini entspringen.

Vom R. alveolaris gehen folgende Aeste ab:

3 Rr. intermandibulares, davon der R. intermand. caudalis zur Haut zwischen den Unterkieferästen (nur bei *Pelusios* versorgt dieser Ast auch den $M.C_1v$ und die Mundschleimhaut), der R. intermand. medius zu Zunge, Mundschleimhaut und Sublingualdrüsen, manchmal führt dieser Ast auch motorische Fasern zum $M.C_1v$, und der R. intermand. oralis zum $M.C_1v$, doch führt dieser Ast zuweilen auch sensible Fasern zu Zunge und Mundschleimhaut.

1 (selten 2) R. cutaneus recurrens, der die Haut der Gelenksregion und um das Tympanon versorgt.

1 R. cutaneus externus, der die Haut lateral an der Mandibel versorgt.

1 R. paralingualis, der vom R.intermand.med. abgeht, aber auch fehlen kann, und zur Mundschleimhaut neben der Zunge führt. Zahlreiche Endzweige des R. alveolaris, die sensibel die Hornscheide des Unterkiefers innervieren.

SYNONYMTABELLE

Chelonia	M. adductor mand. externus	M. adductor mand. posterior	M. pseudo-temporalis	M. pterygo-ideus	M. levator bulbi	Glatter Augen-muskel	M. intermandibularis oralis ($M.C_4v$)
Bojanus 1819—21	M. temporalis	M. pterygoideus				M. palpebralis	M. mylohyoideus
Stannius 1856	M. temporalis	M. pterygoideus internus				M. palpebralis inferior	
Hoffmann 1873—78	M. occipito-squamoso-maxillaris	M. pterygo-maxillaris				M. depressor palpebrae inf. et sup.	M. intermaxillaris
Adams 1919	Capiti-mandibularis	Pterygoideus anterior					
Lubosch 1933	Adductor mand. externus	Adductor posterior	Add. internus temporalis	Add. internus pterygoideus	M. levator bulbi		M. mylohyoideus anterior
Edgeworth 1935	Adductor externus	Adductor mand. medius		M. pterygoid	M. depr. palpebrae inf.		
Edgeworth 1907							anterior mylohyoid
Ruge 1896							C_2mv (part.)
Fuchs 1931							vorderer Teil des M. intermandibularis

VOL. 34 1953

ABKÜRZUNGEN.

a Sehne a
Art Articulare
b Sehne b
Bs Binnensehne
C Ramus cutaneus
C₂dv M. sphincter colli
C₂md M. depressor mandibulae
C₁mv M. constrictor I ventralis (ventraler Trigeminusconstrictor)
C₂mv M. constrictor II ventralis (ventraler Facialisconstrictor)
Ch.t. Chorda tympani
C.m. Cartilago Meckeli
De Dentale
Ff.R.cut.rec. Foramina Ramus cutaneus recurrens
For.trig. Foramen trigemini
Gon Goniale
Int.sept. Interorbitalseptum
Ju Jugale
Ks hornige Kieferscheide
lb Ramus ad labium
Lg Ramus ad linguam
Lig Ligamentum quadrato-maxillare
M. Ramus ad M. intermand. oralem (C_1mv)
M.ang.or. M. anguli oris
Mbm. Mundbodenmuskulatur
Mc Ramus ad mucosam
M.depr.mand.prof. M. depressor mandibulae profundus
M.depr.mand.sup. M. depressor mandibulae superficialis
M.inter. M. intermandibularis
M.intra. M. intramandibularis
M.med. M. adductor mand. externus medius
M.p. M. adductor mand. posterior
Mpl. Mundplatte
M.prof. M. adductor mand. externus profundus
M.pseud. M. adductor mand. internus pseudotemporalis
M.pter. M. adductor mand. internus pterygoideus
M.sup.o. M. adductor mand. externus superficialis origo
N.ang.or. Nervus ad angulum oris
N.intra. Nervus intramandibularis
N.m. Nervus add. mand. ext. medius
N.p. Nervus add. mand. posterior
N.prof. Nervus add. mand. ext. profundus
N.pseud. Nervus add. mand. int. pseudotemporalis
N.pt. Nervus add. mand. int. pterygoideus
N.sup. Nervus add. mand. ext. superficialis
Pa. Parietale
Pfr. Postfrontale
Pro. Prooticum
Pter. Pterygoid
Qu. Quadratum
Quju. Quadratojugale
R.cut.ext. Ramus cutaneus externus
R.cut.rec. Ramus cutaneus recurrens
R.int.c. Ramus intermandibularis caudalis
R.int.m. Ramus intermandibularis medius
R.int.or. Ramus intermandibularis oralis
R.med. Raphe medialis
R.pa. Ramus paralingualis
Socc. Supraoccipitale
Squ. Squamosum
T. Insertionssehne des M. add. int. pseudotemporalis und Ursprungssehne des M. intramandibularis
Tp. Temporalfascie
Tr.Dr. Tränendrüse
Tymp. Tympanon
ZwS Zwischensehne

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VOL.
34
195

THE SEX RATIO IN FARM MINK

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CONTENTS.

Material 294
Results 294
The relation between length of gestation and sex ratio 299
Summary 301
Literature cited 302

OL.
34
953

In species of animals where the sex determining mechanism is chromosomal, the one sex being heterogametic with XY-chromosomes (or XO) and the other sex being homogametic with a pair of X-chromosomes the proportion of males must be 50 per cent "if the two forms of gametes (X and Y, or X and no X) are elaborated by the heterogametic individuals in equal numbers, if these two forms are equally capable of fertilising or being fertilised, and if fertilisation takes place at random . . ." (CREW 1952). However, these reservations only apply to the primary sex ratio, which is defined as the percentage of male zygotes in a sample immediately after fertilization. The few reliable results point in the direction that the primary sex ratio in the fowl (HAYS 1945) and the mouse (MACDOWELL AND LORD 1925) really is 1 : 1, but all investigations concerning the fetal sex ratio indicate a much higher fetal mortality among males than among females (cf. VENGE, in press), at least from the stage of development, where it is possible to distinguish between the sexes morphologically.

The secondary sex ratio is defined as the percentage of males in a sample of newly born individuals. If this ratio "differs from the primary sex-ratio, then a selective prenatal mortality must have been operating between conception and birth" (CREW 1952). Apart from a specific gene action on the meiotic divisions as found in e.g. Drosophila (cf. CREW 1952) only little is known about the causes which induce deviations from equality in the secondary sex ratio. It is often postulated that the sex ratio is influenced by the season, by nutrition, by conception time during oestrus etc., but just as often results are presented where no variation caused by such factors can be found. And seasonal influence is, of course, found only in animals with extended breeding season, but is of no significance in e.g. the mink. A matter which has called the attention of some investigators is the relation between the litter size and the sex ratio. In the pig KRALLINGER (1930) found a tendency to decreasing sex ratio

with increasing litter size when he grouped his material in litter sizes 2—5, 6—9, 10—13, 14—17, and 18—20, the sex ratios being 51.11, 50.99, 50.45, 49.81, and 49.49 percentage males respectively. In the sheep it was shown by JOHANSSON and HANSSON (1943) that the sex ratio decreased from 50.00 for single birth to 49.37 in twin births, 49.13 among triplets and 43.48 in quatruplet births. Despite the insignificance of the difference between the groups two and two the regression of the sex ratio on the number of lambs per birth was significant ($P < 0.001$). APELGREN (1941) found in the mink a sex ratio of 55.8 for single born cubs, but then a rapid decrease to about 50 for litter sizes higher than three. ENDERS (1952) gives the sex ratio in the mink of 104 males to 100 females, i.e. 50.98 per cent males.

In the following some data will be presented concerning the secondary sex ratio in farm raised minks.

MATERIAL.

The data originate from Swedish mink breeders who were requested to make certain observations concerning the physiology of reproduction in the mink. Among these notations, records are available for the litter size, number of live born and stillborn cubs, and generally the sex of the young. Further the date of mating and date of parturition is recorded. The sex determination has in most cases taken place during the first days after parturition, quite exceptionally later on, but in no cases later than the first month after birth. Sometimes young dissappear immediately after birth or during the first days, and in such case no sex determination has taken place. This is the reason that the sex is known only for 11529 of a total of 13262 cubs. To get reliable data concerning the secondary sex ratio in the different litter sizes the material was reduced to comprise only litters where the sex was determined of all young. — Different mutation minks are included.

RESULTS.

For the total material the sex ratio is found to 50.75 ± 0.47, the number of cubs being 5851 ♂♂ : 5678 ♀♀. If the sex ratio is based on the complete litters, i.e. litters with all young sexed, the figure 50.52 ± 0.56 is found. There is no significant difference between these two ratios. The next step in the examination of the material has been to compare the sex ratios for the different variants. The results are presented in table 1. The group "different other types" comprises several mutation minks, most of them belonging to the Silver Blue type (the pp-genotype), but the number in these individual groups has

TABLE 1. *Sex ratio in some different variants of mink.*

Type	All litters			Complete litters		
	Total number of cubs	Number of males	Sex ratio	Total number of cubs	Number of males	Sex ratio
Standard . . .	4927	2522	51.19 ± 0.71	3717	1876	50.47 ± 0.82
Pastel	2572	1264	49.14 ± 0.99	1702	850	49.94 ± 1.21
Crossbred Pastel[1] . . .	2143	1091	50.91 ± 1.10	1316	657	49.92 ± 1.38
Different other types[2] .	1887	974	51.62 ± 1.15	1366	710	51.98 ± 1.35
Total	11529	5851	50.75 ± 0.47	8101	4093	50.52 ± 0.56

been too few to treat them as singles, and no difference in a statistical meaning has been found. From the table, it is seen that there is no difference either between the other groups. The largest difference appears when "different other types" is compared with purebred Pastel (the bb-genotype), but a closer examination has shown that the difference is insignificant ($P = 0.10$). The same is the case when comparison is made between Standard and Pastel, despite the larger number. As a consequence of this it is regarded as permissible to pool the material for examination of the sex ratio within different litter sizes. This is further stressed by the fact that there is no difference with regard to the average litter size between the groups. For Standard the average is 5.02 cubs per litter, for Pastel 5.08 cubs per litter (all Pastels).

The number of litters, cubs and males for the individual litter sizes is presented in table 2 together with the sex ratios. From a high sex ratio in litter size one (54.29) there is a decrease in the excess of males until litter sizes 6—7, but thereafter the sex ratio increases again and reaches 51.43 in litter size 10 and 63.64 in litter size 11. However, the small numbers included in the larger litters (and litter size one) make the averages uncertain, which is seen from the mean errors. A χ^2-test shows no significant deviation from the 1 : 1 ratio, although a decreasing trend in the sex ratio with increasing litter size is found. The regression of the sex ratio on the litter size, computed with due attention to the number of litters, is $b = -0.504$. The regression line is: $y = 53.41 - 0.504\ x$, where y is the sex ratio and x the litter size. This result is in agreement with the findings of JOHANSSON (1932) on sex ratio and multiple births in cattle and JOHANSSON and HANSSON (1943), who found a regression coefficient of —0.569 and a correlation coefficient of $r = -0.791$

[1] Pastel females × males of different types. [2] Females of Silver Blue, Breath of Spring, Aleutian, Halfbred Pastel etc.

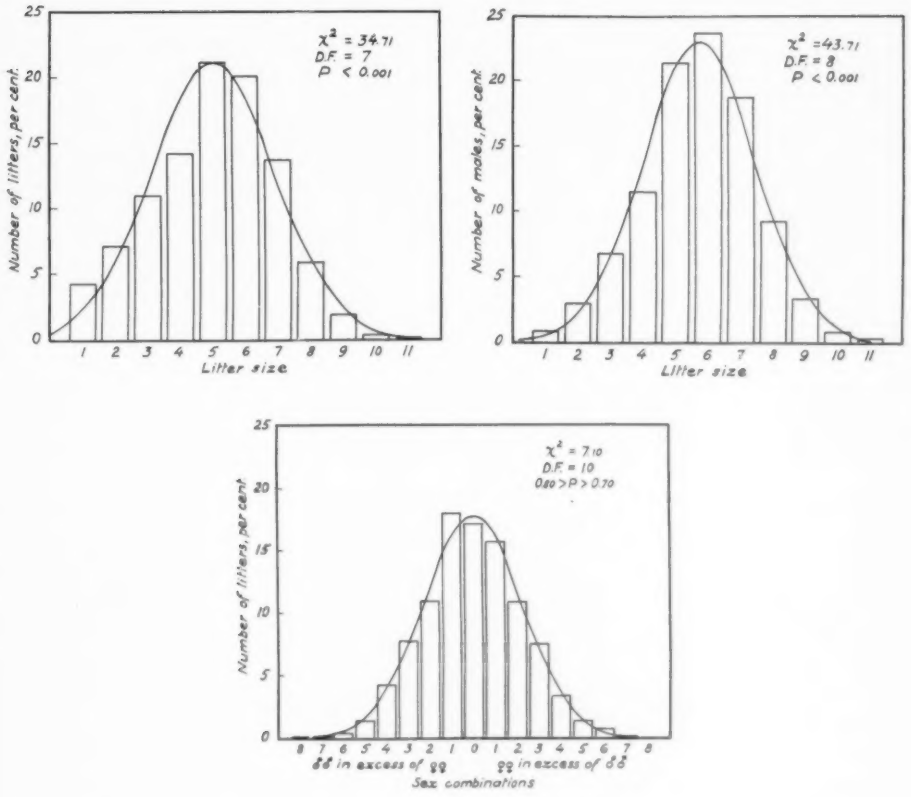
TABLE 2. *Number of litters, cubs and males, and sex ratio in relation to litter size.*

Litter size	Number of litters		Number of cubs		Number of males		Sex ratio
	n	%	n	%	n	%	
1	70	4.33	70	0.86	38	0.93	54.29 ± 8.08
2	115	7.11	230	2.84	121	2.96	52.61 ± 4.54
3	178	11.00	534	6.59	277	6.77	51.87 ± 3.00
4	230	14.22	920	11.36	472	11.53	51.30 ± 2.30
5	343	21.20	1715	21.17	873	21.33	50.90 ± 1.69
6	326	20.15	1956	24.15	973	23.77	49.74 ± 1.60
7	222	13.72	1554	19.18	770	18.81	49.55 ± 1.80
8	95	5.87	760	9.38	381	9.31	50.13 ± 2.56
9	30	1.85	270	3.33	138	3.37	51.11 ± 4.26
10	7	0.43	70	0.86	36	0.88	51.43 ± 8.33
11	2	0.12	22	0.27	14	0.34	63.64 ± 12.86
Total	1618		8101		4093		50.52 ± 0.56

($P < 0.001$) for the sex ratio on the number of lambs per birth. However, it does not seem permissible to use the correlation in this case. Even with the regression coefficient, care must be taken because the variance in sex ratio in the different litter sizes is not constant. A trial has been made to compute the regression under the assumption that the variance is proportional to a certain function of litter size, but then the coefficient is found to +0.634. In spite of the regular decrease in the sex ratio from litter size one to litter size seven, there is a deficit in males in litter size 4. This matter is revealed if the distribution is examined. In fig. 1 and 2 is shown the frequency distribution of number of litters and number of males, and it is seen that besides the deficit of litters as well as males in litter size 4 there is an excess of males especially in litter sizes 6 and 7, while the number of litters with only one cub is also in excess. The reason for this deviation from the normal distribution is difficult to find and it will be hazardous to offer any explanation.

If the conditions hold that fertilization is at random and that no selective mortality during the fetal period takes place, the distribution of the sexes within the individual litter sizes should follow the terms of the binomial $N(p+q)^n$ (e.g. PARKES 1923, BRAMBELL 1944) where N stands for the number of litters of a given size, p and q are the frequencies of males and females respectively, and n is the number of young in the litter under consideration. Table 3 shows the actual number of litters of all different sex combinations (litter sizes 10 and 11 omitted due to the small number) together with the theoretical numbers. The frequencies used in the binomial have been $p = q = 0.5$ in accordance with the view that the two forms of male gametes

VOL 34 195



are elaborated in equal numbers. In no cases have deviations due to other causes than chance been found, despite the tendency towards an excess of males in the smaller litter sizes. If the observed sex ratio (50.52) is used as the frequency in the binomial the agreement is still better. BRAMBELL (1944) tabulated his material on the wild rabbit "according to the excess of the one sex over the other", so that e.g. litters with 5 males + 2 females come in the same class as litters with 4 males + 1 female or 6 males + 3 females, all litter sizes with equal numbers of the two sexes fall in the central class etc. Due to the small numbers involved he further pooled the material to a central class, two intermediate classes and two extreme classes. When grouped in this way he found excess of the number in the central class, while the intermediate classes showed less numbers than expected. When the present material is grouped according to the excess of the one sex over the other the distribution is in accordance with the normal frequency curve (fig. 3). The excess of litters with one male more than females is insignificant, although close to the 5 per cent probability point ($\chi^2 = 2.76$, $0.10 > P > 0.05$).

TABLE 3. *Number of litters of different sex combinations in litter sizes*

Litter size	Combination									Total number of litters
1	1 ♂	1 ♀								70
	38	*32*								
	35	*35*								
2	2 ♂♂	1 ♂ : 1 ♀	2 ♀♀							115
	29	*63*	*23*							
	28.75	*57.50*	*28.75*							
3	3 ♂♂	2 ♂♂ : 1 ♀	1 ♂ : 2 ♀♀	3 ♀♀						178
	23	*70*	*68*	*17*						
	22.25	*66.75*	*66.75*	*22.25*						
4	4 ♂♂	3 ♂♂ : 1 ♀	2 ♂♂ : 2 ♀♀	1 ♂ : 3 ♀♀	4 ♀♀					230
	17	*56*	*92*	*52*	*13*					
	14.375	*57.50*	*86.25*	*57.50*	*14.375*					
5	5 ♂♂	4 ♂♂ : 1 ♀	3 ♂♂ : 2 ♀♀	2 ♂♂ : 3 ♀♀	1 ♂ : 4 ♀♀	5 ♀♀				343
	12	*53*	*116*	*100*	*53*	*9*				
	10.72	*53.59*	*107.19*	*107.19*	*53.59*	*10.72*				
6	6 ♂♂	5 ♂♂ : 1 ♀	4 ♂♂ : 2 ♀♀	3 ♂♂ : 3 ♀♀	2 ♂♂ : 4 ♀♀	1 ♂ : 5 ♀♀	6 ♀♀			326
	3	*38*	*71*	*96*	*83*	*27*	*8*			
	5.09	*30.56*	*76.41*	*101.88*	*76.41*	*30.56*	*5.09*			
7	7 ♂♂	6 ♂♂ : 1 ♀	5 ♂♂ : 2 ♀♀	4 ♂♂ : 3 ♀♀	3 ♂♂ : 4 ♀♀	2 ♂♂ : 5 ♀♀	1 ♂ : 6 ♀♀	7 ♀♀		222
	1	*9*	*44*	*57*	*52*	*47*	*11*	*1*		
	1.73	*12.14*	*36.42*	*60.70*	*60.70*	*36.42*	*12.14*	*1.73*		
8	8 ♂♂	7 ♂♂ : 1 ♀	6 ♂♂ : 2 ♀♀	5 ♂♂ : 3 ♀♀	4 ♂♂ : 4 ♀♀	3 ♂♂ : 5 ♀♀	2 ♂♂ : 6 ♀♀	1 ♂ : 7 ♀♀	8 ♀♀	95
	1	*2*	*12*	*21*	*26*	*16*	*13*	*4*	*0*	
	0.37	*2.97*	*10.39*	*20.78*	*25.98*	*20.78*	*10.39*	*2.97*	*0.37*	
9	9 ♂♂	8 ♂♂ : 1 ♀	7 ♂♂ : 2 ♀♀	6 ♂♂ : 3 ♀♀	5 ♂♂ : 4 ♀♀	4 ♂♂ : 5 ♀♀	3 ♂♂ : 6 ♀♀	2 ♂♂ : 7 ♀♀	1 ♂ : 8 ♀♀	9 ♀♀	30
	0	*1*	*1*	*6*	*9*	*6*	*4*	*3*	*0*	*0*
	0.059	*0.527*	*2.11*	*4.92*	*7.38*	*7.38*	*4.92*	*2.11*	*0.527*	*0.059*

VOL
34
195

THE SEX RATIO IN FARM MINK

THE RELATION BETWEEN LENGTH OF GESTATION AND SEX RATIO.

As is well known the mink is peculiar with regard to the length of gestation. In only few other mammals are found such a tremendous variation in the length of the gestation period as in the mink (cf. the review by HANSSON 1947), and in the present material variation has been noted from 39 days to 68 days. The average length of gestation for females mated only one time is found to be 49.85 ± 0.237 days with a coefficient of variation of 9.69 per cent. Owing to this pecularity the mink should provide possibility for detecting a differential mortality of the two sexes during the intra-uterine period caused by different length of gestation. In order to examine this the material has been confined to females which were mated only one time, because it is only in such cases the exact length of gestation is known. If females are remated one or two times with at least one week's interval 8—16 per cent of the cubs will be from the first mating (JOHANSSON and VENGE 1952), i.e. within the litter there is at least two gestation periods of different length.

In table 4 is presented the sex ratio in relation to the length of gestation for 414 litters comprising 2042 cubs, born by females mated only once. (The extreme classes have been pooled.) By examination of the data it is seen that, with increasing length of gestation there is no systematic increase in the proportion of males. The deviations from the 1 : 1 ratio are insignificant ($\chi^2 = 18.93$, 16 D.F., $0.30 > P > 0.20$). The same applies if the material is grouped in only two classes, the one of which comprising gestation periods between 39 days and 49 days, the other the periods from 50 days to 68 days, or in three classes: 39—47 days, 48—51 days, and 52—68 days. The irregular class-intervals in these treatments has been chosen because it will give approximately equal number of litters in each class. In the first case, such a close agreement between observed and expected values is found, that it will only occur in 2—5 per cent cases ($\chi^2 = 0.002$), while in the other case $\chi^2 = 1.41$ ($0.50 > P > 0.30$). It was suggested above that there was no systematic increase in the sex ratio with increasing length of gestation; that is, generally speaking, that the material grouped according to the length of gestation does not reveal the interdependence between litter size and sex ratio as demonstrated with the previous regression coefficient. The highest sex ratio is found in the groups with shortest gestation which correspond to the largest litters. For the three different classes with short, intermediate and long gestation the following average figures are found:

Gestation period	short	intermediate	long
Sex ratio	51.04	47.92	49.00
Average litter size	5.26	4.85	4.69

TABLE 4. *Sex ratio in relation to length of gestation.*

Length of gestation in days	Number of litters	Total number of cubs	Number of males	Sex ratio	Average litter size
39—42	17	79	48	60.76	4.65
43	14	78	45	57.69	5.57
44	22	104	51	49.04	4.73
45	25	135	59	43.70	5.40
46	26	150	80	53.33	5.77
47	33	175	85	48.57	5.30
48	32	155	78	50.32	4.84
49	45	223	96	43.05	4.96
50	40	189	87	46.03	4.83
51	22	107	62	57.94	4.86
52	27	121	60	49.59	4.48
53	29	139	70	50.36	4.79
54	17	87	45	51.72	5.12
55	15	66	30	45.45	4.40
56—57	17	85	39	45.88	5.00
58—59	18	84	38	45.24	4.67
60—68	15	65	35	53.85	4.33

TABLE 5. *Sex ratio in relation to date of mating.*

Date of mating	Number of litters	Total number of cubs	Number of males	Sex ratio	Average litter size
7/3—15/3	135	685	322	47.01	5.07
16/3—20/3	140	673	329	48.89	4.81
21/3— 2/4	139	684	357	52.19	4.92
$\chi^2 = 3.66$; $0.2 > P > 0.1$.					
7/3—18/3	222	1 083	515	47.55	4.86
19/3— 2/4	192	959	493	51.41	4.99
$\chi^2 = 3.02$; $0.1 > P > 0.05$.					

There is one condition which must be emphasized in the discussion of this material. In all probability it comprises females of different sexual activity. The one category is females which allowed mating only one time, while the other category comprises females which were allowed to mate only one time, and not tried to remate on other days, probably due to lack of males. Unfortun-

VOL. 34 1953

ately, it has not been possible from the schedules to distinguish between these two categories.

To make the analysis of the sex ratio complete the females have been grouped according to the mating date. When the sex ratio is examined for the single mating dates no systematic deviations are found as was the case in the foregoing analysis ($\chi^2 = 12.28$, 16 D.F., $0.80 > P > 0.70$). A grouping of the material in three periods: early mating, mating in the middle of the season and late mating, or in only two periods with early and late mating, indicates a higher mortality among males than females after early mating. The results are shown in table 5. However, no statistically significant deviation from the total average is found. HANSSON (1947) found a greater number of ovulations in the middle than at the beginning and the end of the season. He calculated the average uterine mortality to 49.8 per cent.

Only one comment is to be added to the table. There is no "tendency towards a larger number of cubs after mating in the middle of the season than after mating at the beginning or the end" as suggested by HANSSON (1947). In the present material the highest number of cubs is born by females which were mated early in the season.

Among the stillborn or young dying a short time after birth, the sex has been determined in some cases. Precaution must be taken with respect to these figures because of the small number, but it is doubtful that systematic errors are involved. The total number of dead young of known sex is 196 of which 111 were males, i.e. a sex ratio of 56.63 ± 3.54. This is in agreement with other findings, e.g. JOHANSSON (1932) who found a sex ratio among aborted and stillborn calves of 58.04.

SUMMARY.

Data concerning the secondary sex ratio in the farm raised mink has been presented. The total sex ratio, based on 11529 cubs, is 50.75 ± 0.47 per cent males. When based on litters where the sex of all young was known, the sex ratio was 50.52 ± 0.56 ($n = 8101$). Among stillborn and young died immediately after birth the sex ratio was 56.63 ± 3.54 ($n = 196$). No difference was found between some different variants. The combination of sexes within litter sizes follows the binomial $N(p + q)^n$, where $p = q = 0.5$. When the material was grouped on the basis of the one sex in excess of the other the distribution was normal. The relation between mating date and length of gestation on the one hand and sex ratio on the other was studied in females which were mated only one time. No significant deviation from the 1 : 1 ratio was found. The same applies for the relation between litter size and sex ratio with respect to the single litter sizes. With due attention to the number of lit-

ters the regression of sex ratio on litter size was found to be —0.504, indicating a higher male mortality in larger litters.

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VOL. 34 1953

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4
53